CANADIAN THESES

THESES CANADIENNES

AUTHOR / AUTEUR

BULLARD, J.

MOUNT PROMPTING BEHAVIORS OF...

ISBN

0-315-26995-2

National Library of Canada
Canadian Theses Service
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Services des thèses canadiennes

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL 339 (r. 86/01)

Canada

264

National Library of Canada
Canadian Theses Division
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Division des thèses canadiennes

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

• Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

Bullard, Jeffrey Douglas

Date of Birth — Date de naissance

April 1st, 1956

Country of Birth — Lieu de naissance

Canada

Permanent Address — Résidence fixe

#14 10645 85 ave.
Edmonton, Alta
T6E 2K6

Title of Thesis — Titre de la thèse

Mount Prompting Behaviors of Female Japanese Macaques (Macaca fuscata)

University — Université

University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

Master of Arts

Year this degree conferred — Année d'obtention de ce grade

Spring 1984

Name of Supervisor — Nom du directeur de thèse

Dr. Linda Fedigan

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date

23/02/84

Signature

JDBullard

NL-91 (4/77)

0-315-26995-2

THE UNIVERSITY OF ALBERTA

Mount Prompting Behaviors of Female Japanese Macaques (*Macaca fuscata*)

by

(C) Jeffrey Bullard

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Arts

Department of Anthropology

Edmonton, Alberta

Spring 1984

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Jeffrey Bullard

TITLE OF THESIS Mount Prompting Behaviors of Female Japanese Macaques (*Macaca fuscata*)

DEGREE FOR WHICH THESIS WAS PRESENTED Master of Arts

YEAR THIS DEGREE GRANTED Spring 1984

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

(SIGNED) Bullard

PERMANENT ADDRESS:

#14 10645 35 ave

Edmonton, Alberta

T6E 2K6

DATED Dec 23 19 84

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Mount Prompting Behaviors of Female Japanese Macaques (*Macaca fuscata*) submitted by Jeffrey Bullard in partial fulfilment of the requirements for the degree of Master of Arts.

Linda Marie Fedigan
Supervisor

John T. Hogan

Regna Darnell

A Ellison

Date Feb 23, 1989

Abstract

The vocal and non-vocal communicative behaviors employed by female Japanese macaque monkeys (*Macaca fuscata*) during mating were recorded from September to December 1981 at the Arashiyama West Institute, Texas. Variation in the rates at which females employed these behaviors was analyzed with respect to a number of sociological and contextual variables.

It was found that overall rates of behavior increased with the duration of the intervals between mounts in a series. This finding supports the hypothesis that the behaviors function to prompt the male to mount.

Analysis of the kinds of behaviors employed by different females suggests differences in the prompting strategies of older and younger females. Older females employ less-intense signals as indicators of sexual arousal, resorting to more "volatile" signals when the mating sequence is disrupted. Younger females, on the other hand, employ highly volatile vocal signals in both contexts.

Acoustical analysis of the vocalizations suggests a continuum along both intensity and propagation gradients. The vocalizations employed by older females as indicators of sexual arousal are low on the intensity gradient and show characteristic adaptation for short-range communication. The vocal signals employed by younger females are more intense and show characteristics of signals designed for long distance propagation.

It is hypothesized that the use of signals adapted for distance propagation increases the risk of incidental detection by other males, thus increasing the likelihood of disruption of a mating bout. It is further hypothesized that the observed ontogenetic differences in prompting strategies of female macaques results from increased experience with the negative consequences of the use of volatile, long-range signals during mating.

Preface

I have long considered myself a student of communication. My interests have led me in many different directions. I began my studies by attempting to learn other languages. My exposure to different languages led me to Linguistics where I pursued my interests in the formal structure of language, in a much broader, cross-linguistic perspective.

At the same time, my interests in communication as a multi-modal, interactional process led me to Anthropology and its cross-cultural perspective on communicative interaction. I have "straddled the fence" between these two disciplines ever since.

Through my training in both Anthropology and Linguistics I began to acquire the skills necessary to undertake what I felt to be a much needed integrative study of communication, involving both verbal and non-verbal aspects.

I eventually turned to ethology as a potential method for such an integrative approach. Initially, I was interested in ethology as an observational methodology and its application to human interactional analysis. At the time, I was not overly concerned with the evolutionary perspective inherent in traditional ethology.

In May, 1980, I took an ethology field method's course at the Arashiyama Research Institute in Texas. As I began to study the monkeys at AWI, I became fascinated with the animals and the complex nature of their communicative system, which complexity challenged many of my preexisting notions about animal communication.

I decided to undertake a study of non-human primates for two reasons. First, I saw such a study as an opportunity to gain practical experience with ethological methods. Second, I felt that by studying non-human primates I could begin to gain a cross-species (and possibly a pan-primate) perspective on communication.

I see the communicative systems of non-human primates as alternative systems to human communication. I have also become convinced that comparison of animal and human communicative systems is an essential prerequisite for determining what, if anything, is unique about human communication. Finally, I see the study of non-human

primate communication as necessary to the development of a model from which to hypothesize about the origins and evolution of human language.

The original intent of my research was to investigate the vocal behavior of estrous female Japanese macaques. However, after observing the animals I was dissatisfied with the arbitrary distinction between vocal and non-vocal behavior, since all behaviors were integrated into the communicative system. I therefore decided to look at all communicative behavior. As well, from my initial observations I was struck by the considerable variability in communicative behavior of different females, with respect to both rates and kinds of behaviors. I therefore decided to investigate variation in the communicative behavior of females.

Due to time constraints, it was necessary to confine the study to a specific context; given that females exhibit communicative behaviors in a number of different contexts. I chose the context of mating because it was a highly interactive situation and was fairly easily defined by natural boundaries.

From my analysis, I feel that I have gained significant insights into one small aspect of the communicative system of Japanese macaques as it relates to mating. More generally, my research experience has given me a finer appreciation of the complexities of communicative interactions and the many forces which can influence the communicative process.

Acknowledgements

I would like to extend my sincere thanks to a number of people for their significant contributions to the preparation and completion of this work.

First and foremost, I wish to express my deepest gratitude to Dr. Linda Fedigan who introduced and guided me so skillfully through the vast and fascinating field of primatology. From its very inception, this work has benefitted from Linda's unwaivering support, patience, encouragement, and direction. Both as a teacher and a friend, she has made a lasting contribution to my intellectual development.

I would also like to thank the members of my committee: Dr. Regna Darnell, Dr. John Hogan, and Dr. Carl Urion, who through their discussions and critical readings have contributed to the substantial improvement of this document. This thesis attests to their fundamental contributions to my thinking about communication over these many years.

I am indebted to Dr Larry Fedigan for his invaluable support and advice which I have sought throughout all stages of this work. His wit and friendly "goadings" helped me to overcome frequent inertia.

Without the unstinting assistance and tireless enthusiasm of Colin Chapman, this thesis would surely not have been completed on time. Colin's much valued criticism helped to strengthen my arguments considerably.

I wish to thank the Arashiyama Research Institute for granting me permission to conduct my research. Were it not for Lou Griffin, general manager of AWI, I could easily have given up in my many moments of despair and self-doubt. Her friendship and advice made my stay in Texas a rewarding one. I would also like to thank fellow AWI researcher Mary McDonald, who generously shared her observations and comments with me. Mary's own research played an important role in the completion of this thesis.

I owe a special thanks to Drs. Harold and Sally Gouzoules for their hospitality and advice during my visit to the Rockefeller Research Station. Their work on non-human primate vocalizations continues to be an inspiration to me.

Numerous people in the Department of Anthroplogy have been especially helpful. Rick Will, friend and mentor, challenged many inconsistencies in my arguments. His preparation of the figures is also greatfully acknowledged. Becky Cole-Will ensured the speedy and accurate preparation of the manuscript, providing substantive criticism. Many thanks to Joel Minion and Nancy Collinge for their encouragement right down to the wire. The Department of Anthropology generously provided financial assistance, office space, and computer facilities.

In my "second home", the Department of Linguistics, I wish to particularly thank Peter Assman who provided me with constant consultation and assistance on the acoustical analysis. Through his fine appreciation and knowledge of animals, and his expertise in acoustics he gave me invaluable direction. Dr. Terry Nearey deserves credit for preparing me for the task of analyzing the vocalizations. I appreciate his comments and suggestions. Tracey Derwing and Murray Munroe provided encouragement and editorial advice. The Department of Linguistics kindly allowed me access to its laboratory facilities.

As always, I am thankful to John Gole for the many personal sacrifices he made and for the stability he provided; enabling me to carry through with this project.

Financial support is greatfully acknowledged from the following: the Department of Anthropology in the form of a Teaching Assistantship (1980), and the Government of Alberta from a Province of Alberta Graduate Scholarship (1981) and a Ralph Steinhauer Award (1982-1984). Funding was also provided through Dr. Fedigan's NSERC grant (#A7723).

Finally, I would like to thank the monkeys at AWI for tolerating my presence among them.

Table of Contents

Chapter — Page

Abstract iv

Preface v

Acknowledgements vii

List of Tables xi

List of Figures xii

I. Introduction 1

A. Introduction 1

B. Objectives 4

C. Problem 4

II. Background and Initial Observations 6

A. Introduction 6

B. Study Species 6

Breeding Season 7

Consorts 8

Mating 8

C. Vocal Advertisement 9

D. Female Solicitation 10

E. Mounting 11

Heterosexual Consorts 11

Homosexual Consorts 16

F. Problem 17

G. Sociological Variables 18

Kinship 18

Age 18

Parity 19

Maternal Status 20

H. Contextual Variables 20

Partner Age-class 21

Interval Duration 22

III. Methods 25

A. Study 25
Study Troop 25
Study Site 26
Study Population 27
B. Sample 28
C. Data Collection 30
Focal Animal 30
States 31
Events 31
D. Recordings 34
Vocalizations 34
E. Hypotheses 36
F. Data Analysis 36
Behavioral Data 36
Statistical Tests 40
Acoustical Data 40
IV. Analysis and Results 43
A. Acoustic Analyses 43
Hacks 43
Geckers 43
Screams 47
Other Calls 58
Discussion 60
B. Behavioral Analysis 63
Sociological Variables 63
Contextual Variables 67
Discussion 69
V. Conclusions 71
A. Discussion 71
B. Summary 78
Bibliography 79

List of Tables

Table : Page

Table 1 :

Reported Intermount interval Duration 13

Table 2 :

Study Sample Distribution 29

Table 3 :

Descriptive Statistics of Mating Bouts 38

Table 4 :

Rates (per 10 Seconds) of Prompting Behaviors 41

Table 5 :

Vocalizations Along Intensity and Propagation Gradients 62

Table 6 :

Differences in Mating and Prompting Behaviors 64

Table 7 :

Differences in Specific Prompting Behaviors 65

List of Figures

Figure Page

Figure 1 :

Distribution of Between-mount Interval Durations 39

Figure 2 :

Wideband Sonagram of Hack Vocalization 44

Figure 3 :

Wideband Spectral Section of Hack Vocalization 45

Figure 4 :

Wideband Sonogram of Gecker Vocalization..... 46

Figure 5 :

Wideband Spectral Section of Gecker Vocalization..... 48

Figure 6 :

Wideband Sonagram of Simple Scream Vocalization 50

Figure 7 :

Narrowband Sonagram of Simple Scream Vocalization 51

Figure 8 :

Wideband Spectral Section of Simple Scream Vocalization..... 52

Figure 9 :

Wideband Sonagram of Defensive Scream Vocalization 53

Figure 10 :

Wideband Sonagram of Scream/ Gecker Vocalization 55

Figure 11 :

Wideband Sonagram of Prolonged Gecker Vocalization..... 57

I. Introduction

A. Introduction

Recent advances in the field of non-human primate vocal communication have necessitated reexamination of prevailing opinions concerning the nature and complexity of animal communication. Employing the methodology and technology of Acoustic Phonetics, primatologists have begun to investigate the complex, acoustical properties of non-human primate vocal signals, revealing much about the encoding of information. The use of sonograms, which permits detailed acoustical analysis of signals, is now commonplace in vocalization research, having gained widespread acceptance since the pioneering work by Rowell and Hinde (1962). More recently, researchers have begun to synthesize non-human primate vocalizations, testing differences in response to manipulations of various parameters of the signal. (Waser, 1975; Waser and Waser, 1977)

Acoustical analysis of the vocalizations of non-human primates has demonstrated a rich array of encoded information, revealing much about the complex nature of monkey social interactions. One of the most recent and extensive reviews of non-human primate communication research, Primate Communication (Snowdon, et al., 1982) bears witness to both the sophistication and diversity of current research. One of the notable gains in non-human primate vocal communication research has been in the categorization of vocalizations on the basis of 'meaningful' variation in acoustic parameters.

Previously, vocal 'repertoires' of non-human primates had been characterized as small sets of stereotyped or invariable signals, highly constrained by context. Researchers catalogued the calls of a given species, noting the context(s) of occurrence of call types. Calls were usually labelled on the basis of gross perceptual characteristics such as loudness and pitch. Very often, calls were labelled on the basis of perceived similarities with human speech sounds (Itani 1963). Researchers concentrated on establishing differences in function and meaning of calls; variation within call types was

seen as random or non-meaningful. However, researchers have recently begun to investigate previously ignored acoustical variation within call types, revealing recurrent, meaningful patterning.

It has long been recognized that variation in form and usage of human speech by members of a community can reflect structural and organizational principles within that community. The dynamics of language change (Labov 1972), the structure of social relations (Thibault 1979), and the principles governing interaction between individuals (Hymes 1974) have all been approached through the analysis of variation in speech. The analysis of variation in the communicative behavior of non-human primates can similarly yield insights into their social organization.

For example, analysis of the variation in 'grunt' or 'woof' vocalizations of vervet monkeys (*Cercopithecus aethiops*) given by different animals in different contexts, has shown hitherto unrecognized patterning (Cheney and Seyfarth 1983). The 'grunt' vocalization had been described as an acoustically variable call given in a variety of contexts, most notably when one animal approaches another (Struhsaker 1967), however, until recently, the variability was left unexplored. Cheney et al. demonstrated that 'grunts' given in different contexts were acoustically different, and elicited quantifiably different responses when played back to individuals. Subjects either a) moved away or, b) oriented themselves to the source in a variety of ways depending on the type of vocalization played. Detailed acoustical analysis has revealed that the grunts given in different contexts have different acoustical structures, eg. the position of amplitude peaks varied. On the basis of these experiments, the researchers differentiated at least five types of 'grunts' from the previously described single-category call. This research provides new insights into information encoding in non-human primate vocalizations. The research also suggests a much more sophisticated, complex system of vocal communication than has previously been assumed.

The work by Gouzoules and Gouzoules (1983) on the juvenile screams of rhesus macaques is another example of documented patterning in variation which had previously been overlooked. The scream vocalizations given by rhesus monkeys (*Macaca mulatta*) in agonistic interactions had been described earlier and extreme acoustical variation had been noted (Rowell, 1962; Hinde and Rowell, 1962). The observed variation was explained in

terms of graded signals along a continuum of intensity. Following the playback protocols established by Seyfarth et al. (1983), the Gouzoules were able to elicit differential responses of mothers to screams of their offspring given in different contexts. Subsequent acoustical analysis of the vocalizations given in each of the contexts revealed consistent structural differences. The Gouzouleses were able to document five discrete scream vocalizations given by juvenile rhesus in agonistic interactions. These screams encode such complex information as a) the rank of the opponent relative to the caller's rank, b) the relatedness of the opponent, and c) the presence or absence of physical contact with the opponent.

As evidenced in the examples above, the analysis of variation in the <u>form</u> of vocalizations can yield important information about the nature of vocal communication. Variation in the <u>use</u> of vocalizations by different individuals (or classes of individuals) can also provide information about vocal communication, by elucidating those sociological and contextual factors which coincide with an animal's communicative behavior.

Green's (1975, 1981) work on the vocal communication of Japanese macaques (*Macaca fuscata*) demonstrates how the analysis of variation in signal usage can enhance our understanding of non-human primate communication. His research on the 'coo' calls of Japanese macaques (1975) focuses on the acoustic nature of the calls and the contexts in which they are used, in an attempt to determine the 'meanings' of different vocalizations. Green identified several acoustically distinct but structurally related classes of calls within a previously undifferentiated category of vocalization. Acoustic differences between these classes of 'coo' calls were seen to reflect differences in the 'arousal level' or motivational state of the animal. Green found a statistically significant correlation between the structures of 'coo call' types and those contexts "...in which the demeanor, arousal, social spacing, and orientation of the vocalizing animals are similar". (Green 1975:72). Green's work is an important step in understanding the role of context in non-human primate communication.

Green (1981) has also looked at variation in the use of specific vocal signals by different individuals or classes of individuals. The use of particular vocalizations may be restricted to, or more common among, certain classes of individuals. Green identified one type of Japanese macaque vocalization, the "long call", which was given exclusively by

adult males. Other vocalizations were described as being more common, i.e. occurring more frequently, among juveniles, etc. Green's preliminary analysis of variation in the use of specific vocalizations suggests that vocal behavior may reflect certain ontogenetic, and sex or role related differences in non-human primate societies.

B. Objectives

The main objective of this study is to describe the vocal and non-vocal communicative behavior of female Japanese macaque monkeys in the specific context of mating, attempting to explain the function or evolutionary advantage (Jolly, 1972) of these behaviors. Variation in the use of specific behaviors by different females will be analysed with respect to sociological and contextual factors. Differences in the acoustic characteristics of the vocalizations employed by females will also be explored.

C. Problem

It has been noted by many researchers familiar with Japanese macaques (Fedigan 1982; Wolfe 1976; Gouzoules pers. comm.) that there is a marked increase in the vocal behavior of females during the breeding season. Vocal behavior varies with respect to specific contexts, such as partner solicitation, vocal advertisement, and mating. Within the context of mating, there is considerable variation in the communicative behavior exhibited by females, e.g. some females vocalize more than others, some employ more non-vocal behaviors, etc. However, to date there is very little documentation on the nature and extent of this variation beyond anecdotal observations.

Analysis of female macaque communicative behavior during mating must necessarily make reference to both physiological and contextual aspects of the mating system. For example, the work by Zumpe and Michael (1968) on the behavior of female rhesus macaques during a mount, suggests that the frequency with which the behaviors are employed reflects increasing sexual arousal in females, due to increased stimulation through a series of successive mounts. Because there has been no coherent model of the macaque mating system of 'series' mounting from which to interpret observed behavior,

most of the work on communicative behavior in the sexual context remains at the level of description.

Based on field observations and a review of the literature, this thesis will attempt first to describe the general pattern of vocal (and non-vocal) communicative behavior of estrous female Japanese macaques in various consort-related contexts during the breeding season (Chapter 2). This general overview is then followed by an indepth analysis of the variation in the vocal and non-vocal communicative behaviors exhibited by females during actual mating. The degree and nature of observed differences between females is examined, and the extent to which contextual and sociological factors account for the differences is investigated.

Methods employed in the collection of frequency data and audio recordings of vocalizations are described in Chapter 3. Chapter 4 details the results of the acoustical analysis of the vocalizations, followed by a discussion of the results from the analysis of frequency data. Chapter 5 summarizes the findings from this study, and offers some hypotheses about the function(s) of the communicative behaviors exhibited by females, with reference to a proposed model of 'series mounting'. Finally, some conclusions are drawn about the process of ontogeny and learning on the use of vocal and non-vocal behaviors by female Japanese macaques during mating.

II. Background and Initial Observations

A. Introduction

The genus *Macaca* is one of the most extensively studied of all the non-human primate taxa, due in large part to the fact that macaque species have been relatively easily procured for laboratory use for some time. The rhesus macaque (*Macaca mulatta*) from India, in particular, has been used extensively in medical research in North America for over 50 years. Increasing restrictions on the export of rhesus macaques led to a subsequent increase in the use of other closely related macaque species: it is not uncommon to find a variety of macaque species housed together in laboratories. The Japanese macaque, while commonly used in lab studies, have also been studied extensively in their natural environment. Japanese primatologists, in particular, have undertaken longitudinal studies of *Macaca fuscata* for the past 30 years, yielding much information about their ecology, behavior, and social organisation.

Sexual behavior is perhaps the single most studied aspect of Japanese macaque behavior. The emphasis on sexual behavior is, in part, due to the fact that Japanese macaques exhibit a discrete breeding season, elaborate courtship displays, consort bonding, and a complex mating system involving series mounting. Following is a general overview of the ecology, social organisation, breeding season, and mating system of Japanese macaques.

B. Study Species

Japanese macaques are endemic to the islands of Japan. They are the most northerly ranging non-human primate. They are adapted to cold winters and often encounter snow throughout the northern extremes of their range; hence the popular name "snow monkey". These monkeys are semi-terrestrial, and their diet typically consists of buds, shoots, leaves, bark, nuts and berries. They live in large multi-male, multi-female

groups; comprised of matri-focal units and a central core of adult males. Japanese macaques exhibit a discrete breeding season of three to four months, followed by a birth season approximately six months later.

Breeding Season

During the breeding season, mature Japanese macaques exhibit observable physiological and behavioral changes.

> The two early cues to the on-coming mating season in these macaques are conspicuous reddening of facial and perineal skin, and a conspicuous rise in the number and the intensity of agonistic interactions, particularly those initiated by adult males (Fedigan, 1982 p. 138).

Indeed, a significantly higher incidence of serious physical wounding occurs during the early stages of the breeding season. Wolfe (1976) notes an increase in the size of male testes associated with the breeding season, which she attributes to the onset of spermatogenesis, and Eaton (1976) reports higher levels of testosterone among adult males during the breeding season. Although there is some variation between individuals, males become sexually mature at approximately four and one half years (Hanby et al., 1971; Hanby, 1972; Nigi et al., 1980; Rostal and Eaton, 1983). Behavioral changes in males are evident in the breeding season as well. Of particular note are the elaborate courtship displays of males.(Modahl and Eaton 1977; Stephenson, 1973; Tokuda, 1962)

> Adult males may launch lightning-speed attacks on females and run off ...or they may attract her attention with long-range tree shaking displays, or close range weaving-and-strutting displays, occasionally involving branch dragging (Fedigan, 1982; pp.138-139).

Females too, undergo physiological and behavioral changes associated with the breeding season, such as reddening of the face and perineum, and in young females some swelling of the perineum (Tokuda, 1962). Females generally reach sexual maturity earlier than males, often starting to exhibit sexual behavior at about three and one half years (Nigi, 1976; Wolfe, 1976). Behavioral changes include increased agonistic encounters and solicitation. Unlike the changes in males, however, females do not exhibit these physiological and behavioral changes constantly throughout the breeding season. Rather, these changes are associated with periods of estrus: "...estrus is female motivation (proceptivity) and/or willingness (receptivity) to mate" (Fedigan, 1982; p. 140). Estrus is a complex behavioral and physiological phenomenon: it is not necessarily linked with

ovulation (Wolfe 1976), nor conception (Fedigan, 1982). Estrus "does not always occur on a regular cyclic basis, or in correlation with known endocrine states, but always does imply periodic rather than continual willingness to mate" (Fedigan, 1982; p. 140). The duration and number of estrus periods during a breeding season is highly variable for an individual and between individuals. What remains constant, however, are the unmistakable signs of estrus exhibited by all females.

Consorts

During the breeding season, animals will form consort relations with a number of partners. A consort is defined as a temporary, exclusive attachment between two individuals (Fedigan, 1982; Tokuda, 1962). The length of a consort is extremely variable, lasting from a short period in a day up to two weeks. A female will typically establish a series of consorts with a number of males during each estrous period. A couple will usually have several "mating bouts" during a consort. Contrary to the long held opinion that macaques are "randomly promiscuous", there is some evidence for constancy from one year to the next with respect to consort partners (Baxter and Fedigan, 1979). Consorts are generally sequential, and mating is usually exclusive. While in consort, partners will often remain in close proximity, even when not mating.

Mating

Japanese macaques are "series" mounters; a "copulation" or "mating bout" consists of a series of mounts, each involving intromission and multiple thrusting. In a heterosexual consort, a mating bout culminates in male ejaculation after several successive mounts. The number of mounts in a bout is variable. (For a detailed discussion of mating, see below.) Homosexual consorts between females are a common occurrence during the breeding season as well. These consorts adhere to the general pattern of heterosexual consorts, although there is considerable variation with respect to number and timing of mounts, and duration of bouts, due to a high degree of reciprocal mounting and the absence of a culminating ejaculatory mount. (See Homosexual consorts below.)

The concern of this thesis is with the communicative behavior of estrous female macaques. There are several specific contexts during which estrous females exhibit

characterisitic patterns of vocal and non-vocal behavior: early estrous "vocal advertisement", pre-consort female "solicitation", and mounting (both heterosexual and homosexual consorts). Following is a description of each of these contexts, and the patterns of female communicative behavior associated with each, based on a review of the literature and my own field observations.

C. Vocal Advertisement

An estrous female can sometimes be found sitting away from the central troop, uttering long sequences of a variety of vocalizations. This behavior is characteristic of pubescent females, and younger females. This behavior most often occurs during the early stages of estrus, prior to courtship and the establishment of a consort.

Itani (1963), in his article on the vocal communication of Japaese macaques, describes the behavior as follows:

> While the troop are feeding, a female in estrus, rather young, sitting alone on a tree-top in a thicket a little away from the central part of the troop, emit these sounds for a long time. It is not a call to a certain individual, but a very self-centered manifestation of emotion. The voice now and then changes to an unstable tone belonging neither to a type intermediate between other sounds nor to a transitional type, and the sounds of B-group [defensive] and C-group [agonistic] frequently occur throughout the series. (p 51)

Fedigan (1982) has also observed this behavior in young estrous females:

> They often move away from the other group members and sit alone in the brush screeching loudly, or they may appear to run quickly through their repertoire of Japanese macaque vocalizations, from weaning sounds to alarm calls (p 138).

My own observations suggest that these vocalization bouts include a large repertoire of call types. It is very characteristic in the utterances to have calls juxtaposed which would normally be interpreted as reflecting contradictory states. A female might utter a series of screams (normally indicating intense motivation) punctuated by contact calls (normally associated with low intensity, close-proximity interactions), suddenly switching to alarm calls or threats.

There is as yet no clear understanding of the function of this behavior. Fedigan (1982) suggests that this behavior may serve as a form of "vocal advertisement", indicating the female's estrous state as a preliminary to courtship. It may even be, as Itani (1963) suggests, a form of release for young females experiencing confusing emotional and

physiological changes. In any case, this behavior cannot be seen as a direct form of female solicitation, as both authors indicate that when approached by a male, a female exhibiting this behavior will immediately flee. My own observations lead me to conclude that this behavior reflects a nervous young female's attempt to attract a male. After following a particular female for some time as she exhibited this behavior it became apparent that she was monitoring the movements of a male, following him yet maintaining a safe distance. When the male approached her, however, she fled.

D. Female Solicitation

The majority of research on Japanese macaque "courtship" has concentrated on male behavior. This bias is due in large part to the very stylized and complex displays exhibited by adult males (Fedigan, 1982; Modahl and Eaton, 1977; Stephenson, 1973). Female macaque courtship or solicitiation, which is somewhat less dramatic than male behavior, nevertheless does occur (Cochran, 1979; Green, 1975). A recent investigation by McDonald (1983) on the pre-consort solicitation behaviors of female Japanese macaques provides further evidence which indicates that females do actively court and select consort partners.

A female will follow a particular male, attempting to decrease the distance from the male. Various "stages" in this process of decreasing distance have been described (McDonald, 1983; Stephenson, 1973), and the behaviors exhibited by females during the different stages of solicitation vary. Females employ a variety of vocalizations and non-vocal behaviors when soliciting a male.

Green (1975) has demonstrated that female macaques employ different types of "coo" calls at various stages throughout the solicitation process.

> Dip late highs accompany the very earliest stages of female inititiated courtship solicitations, and are rare at the later stages. The next type, the smooth late high coos, has the converse usage. They are the more frequent accompaniments of the somewhat advanced stages of solicitation (pp 27-28).

McDonald (1983) observed changes in the repertoire of non-vocal behaviors employed by females in the various stages of solicitation as well. She found that females of different ages showed differences in both the frequency and type of behaviors employed during solicitation. McDonald characterizes the solicitation behavior of younger females as

extremely agitated or "frantic" as compared to the more controlled or "sophisticated" pattern of older females. She suggests that the differences observed between younger and older females can be explained on the basis of learned behavior: older females employ behaviors which will reduce or diminish negative responses by males. Many of the communicative behaviors employed by females in the later stages of solicitation are also used in the initiation and maintenance of mating and consort bonds (Cochran, 1979).

E. Mounting

Heterosexual Consorts

A mount sequence is generally short in duration. The female stands quadrupedally. The male clasps the upper calves of the female with his hind feet and places his hands on the female's back; a double foot clasp mount. Some variation in the male-mount-female position can be observed, including a male standing with his hind feet on the ground, and even some ventral-ventral mounts have been observed, usually among younger animals (Stephenson, 1973). The female raises her tail to facilitate intromission. A mount sequence culminating in ejaculation is generally longer than other sequences, due to a noticeable pause in the thrusting associated with ejaculation. After ejaculation, the male will move several feet away, where he will sit and groom his genitals; removing and eating residual ejaculate. The female sits and grooms her genital area as well.

The female usually remains stationary during a mount sequence, although she may exhibit certain characteristic behaviors such as: turning and looking at the male, fear grimacing, reaching back with one arm and grabbing the pelage on the chest of the male. On some occasions, the female may reciprocally mount the male. The female can also vocalize at some point during the mount sequence. When a male mounts a female she may vocalize as she stands for the mount. As well, the female may vocalize at some point while the male is mounting, or just as the male is dismounting. Finally, if a female immediately mounts the male after the male dismounts, the female mount is almost invariably accompanied by vocalization. The vocalization employed during mounts are almost uniformly "geckers", although some "hacks" were recorded.

Studies of female behavior during a mount sequence have suggested that these vocalizations are expressions of female sexual arousal and orgasm (Zumpe and Michael, 1967; Goldfoot et al., 1980). As well, Deputte and Goustard (1980) found that variations in the structure of vocalizations emitted by female crab-eating macaques *(Macaca fasicularis)* during mounts, reflected differences in levels of female sexual receptivity or motivation.

The between-mount interval is a period of general quiesence between mount sequences. The animals sit beside or against one another. The most typical position is for the male to sit with legs apart against the haunches of the female. On some occasions, especially, but not exclusively with younger males, the male will masturbate. On one such occasion I saw a fully adult male masturbate to ejaculation during a between-mount interval. Sometimes, the male will leave the female, display on a nearby tree or some other structure, then return to the female. The duration of between mount intervals is variable.

There are interesting differences in the literature with respect to the degree of variation in the duration of intervals between the mounts in a series. Some researchers (Eaton, 1978; Tokuda, 1962; Wolfe, 1976) characterise the intervals as relatively constant, whereas my own observations (see Chapter 3) and those of Carpenter (1942) suggest considerable variation in interval duration. Table 1 shows reported values for between-mount intervals from available sources.

Differences in the interval values may reflect differences in the exogenous forces acting upon mating bouts in the samples, e.g. higher incidences of mating disruption or the effects of male lethargy (see below). Interestingly, McClintock et al. (1978) indicate that under restrictive conditions (e.g. small cages) interval timing and female behavior are extremely invariant in series-mounting rodents, but that when environments reach near-natural conditions they found considerable variation in both interval duration and female patterns of behavior. However, while this finding might account for the relatively invariant values reported by Eaton (1978) for the animals at the Oregon Primate Centre, which are housed in relatively restricted environments, the values reported by Tokuda (1962) and Wolfe (1976) were based on observations of animals in more natural conditions. The differences in values between my own observations and those reported

Table 1 Reported Inter-mount Interval Durations

Author	Species (location)	Mean	Range	Comments
Bullard[1] (1983)	M. fuscata (AWI)	46.9 sec	1-600 sec	extremely variable
Carpenter (1942)	M. mulatta (CAYO)	--	<1-20 min	extremely variable
Eaton (1978)	M. fuscata (OREGON)	1.5 min	---	relatively constant
Tokuda (1962)	M. fuscata (KOSHIMA)	--	13-47 sec	constant
Wolfe (1976)	M.fuscata (AWI)	--	10-50 sec	constant

1. Intervals >600 sec are not included in the sample.

by Wolfe (1976) are especially puzzling, given that they are based on observations of the same group of monkeys. (Indeed, my results are based on observations of the group after they had moved to a smaller enclosure from the one they were in during Wolfe's study.)

Interruptions can and do occur during a mating bout. Perhaps the most common disruption is for a female to be chased away from her partner by another male. The focus of the attacking male is clearly the female; male-male conflicts in these situations are rare. The female's partner will often simply remain in place or casually follow in the direction of the female. In some cases, however, the male partner will even join in the attack of the female. An outside male need not necessarily attack. Very often, his presence in the general vicinity is enough to make the female flee. When disrupted by another male, females will emit a long series of vocalizations, including screams, defensive screams, and threats. Major disruptions which affect the whole troop, such as the arrival of the provisioning truck or a predator, will disrupt mating bouts as well. Other, less disruptive interruptions can occur which can cause a delay in the mating sequence i.e. prolong a between-mount interval. A male may leave the female then return. One of the most common causes of a delay is male lethargy. Males often exhibit signs of fatigue; especially later in the breeding season, and especially with males who have been extremely sexually active. These males often seem to sleep for long periods between mount sequences.

Female behavior is extremely variable during between-mount intervals. Very often, a female will doze, groom (herself or her partner), idly forage on plants within easy reach, or simply sit quietly throughout the entire interval. At other times, the female may turn and look at the male, manipulate a nearby object, slap the ground, present for mount, or even mount the male. The female may also vocalize, both independently and in conjunction with these other behaviors.

Michael and Zumpe (1970) investigated the behaviors of female rhesus macaques during mating. They compared the behaviors of females before, during, and following a mating bout. They found a correlation between female behaviors and male mounting activity, supporting the view that the behaviors are employed to prompt males (Carpenter, 1942). However, they were unable to explain the considerable variation between females

in the use of specific behaviors. For example, one female showed a marked increase in the use of "presentations" during the mating sequence, the second female rarely employed this behavior at any time, and the third female showed a decrease in the use of "presentations" during mating (although this female did use other behaviors which correlated with male mounting). The two most serious problems with this study are a) the small sample (N=3), and b) the fact that the researchers did not distinguish between those behaviors used during the mount, and those used between mounts.

A second study by these same researchers (Zumpe and Michael, 1977) investigated the influence of male ejaculation on the frequency of behaviors exhibited by females during a mating bout.

> Comparison of the number of sexual invitations in pairs of successive tests showed that tests without ejaculation following those in which ejaculations occurred were associated with increased numbers of invitations; conversely, ejaculatory tests following non-ejaculatory tests were followed by decreased numbers of invitations (p 275).

Once again, there were differences in the patterns of behaviors exhibited by different females which were not explained: two of the subjects mainly employed "presentations", while the third subject employed a wide variety of behaviors. The researchers also noted that two of the females

> made more invitations with the partner that tended to ejaculate most frequently while [the other] female...made more invitations with the partner that tended to ejaculate less frequently (p 270).

As with the previous study, the sample size was small (N=3) and behaviors employed by females during and between mounts were not differentiated. Given that the behaviors exhibited by females in the two contexts have been argued to serve different functions (the behaviors exhibited during mounts indicate sexual arousal, whereas the behaviors exhibited between mounts function to prompt the male) grouping all behaviors exhibited by females, regardless of context, does not seem appropriate. Finally, in neither of the studies was reference made to the vocal behaviors exhibited by females during mating, although such behaviors have been reported to occur. As yet, the observable differences between females in the use of various communicative behaviors during between-mount intervals in a mating bout have not adequately been explained.

Homosexual Consorts

The occurrence of female-female consorts in *Macaca fuscata* is fairly common (Gouzoules and Goy, 1983; Stephenson, 1973; Wolfe, 1976) There is, however, variation in the frequency of occurrence from group to group. Studies of female homosexual behavior in the Arashiyama West group suggest that the phenomenon cannot be explained in terms of shortage of mature males (Gouzoules and Fedigan, 1979). Females who engaged in homosexual consorts were also found to have engaged in a high frequency of heterosexual consorts, and can generally be said to have had a very active season. The researchers suggest that homosexual behavior is an expression of an overall pattern of heightened sexual activity, usually occurring among females who did not have an infant from the immediately preceeding birth season.

Female-female consorts are extremely active; they demonstrate the highest degree of reciprocal mounting. They are also the "noisiest" consorts during the breeding season. This impression is undoubtedly due to the fact that both partners vocalize throughout a mating bout (unlike heterosexual consorts in which males usually remain silent).

Homosexual consorts follow the general pattern of series mounting demonstrated in heterosexual consorts. There is more variation in the mount positions employed by females during a mount sequence. The most common position is the hip straddle; the female sits on the back of her partner, straddling her partner's hips and rubs her perineum against her partner's back. Ventral-ventral mounting is also quite common in homosexual consorts.

During a mount, females demonstrate the same behaviors as with heterosexual mounts. The females being mounted can look back, reach back, and vocalize while being mounted. The female mounting will often vocalize as well.

The interval between mounts in homosexual mount sequences appears to be very erratic. In heterosexual consorts mounts generally occur at regular intervals and the animals are normally quiescent. In homosexual consorts the intervals seem irregular and the animals much more active. Females seldom sit very long between mounts. One or the other of the partners may begin to leave, looking back at the partner. A characteristic behavior associated with homosexual consorts is for a female to approach the observer, vocalizing and looking back at her partner. The vocalizations recorded include screams,

threats and alarms. Very often a female would actually sit beside the observer and tug on his pant legs, all the while vocalizing and looking at her partner. This behavior would be followed by the partner quickly approaching and mounting the female, vocalizing as she approached. As with the case of 'slap ground', 'manipulate object', etc. I would argue that 'approach observer' functions as a prompting behavior. Although not exclusive to homosexual consorts, from my observations I would conclude that "approach observer" was less frequently employed by females in heterosexual consorts and never with the same intensity, i.e. females with male partners never approached as close to the observer.

F. Problem

The task of analysing differences in the communicative behaviors of estrous females for each of the above contexts far exceeded the limits imposed on this study by time constraints. As indicated above, some initial attempts have been made to investigate the behaviors exhibited by females during heterosexual mating bouts. While there is some fairly conclusive evidence as to the function of female behaviors during actual mounting, i.e. they reflect increasing levels of female arousal resulting from stimulation through repeated intromissions, little is known about the behaviors exhibited by females in the intervals between the mounts in a series, beyond the general hypothesis that they serve to elicit mounting. In particular, the high degree of variation in the use of specific behaviors by different females as yet remains unexplored. Consequently, it was decided to investigate the variation in patterns of vocal and non-vocal behaviors of estrous females in the between-mount intervals of heterosexual mating bouts. For this study, it was decided to analyse the influence of specific sociological and contextual variables which might account for observed differences between females, at the same time increasing the sample size over previous studies.

G. Sociological Variables

The validity of certain sociological variables for explaining differences in behavior has been demonstrated time and again in non-human primate research (Bramblett, 1978; Jolly, 1972). Animals with a given sociological characteristic in common may exhibit similar patterns of behavior, and these animals also exhibit a different behavior pattern from other groups. The sociological variables to be investigated in this study are: kinship, age, parity, and maternal status. These variables will be discussed in detail below.

Kinship

There is common agreement among researchers who have worked with the Arashiyama West monkeys that not only do certain related individuals bear a strong physical resemblance to one another, but that some related individuals even sound alike (Griffen pers comm.) The Wania family, for example, are recognized for their characteristic food-call vocalization. The matriarch, Wania, and her granddaughter both have easily identifiable, similar voices and styles of vocalizing. Thus, it is not unreasonable to infer that kin-related females may demonstrate similar patterns of behavior in between-mount intervals of mating bouts. Do females of a particular kin-line vocalize or employ non-vocal behaviors more frequently than others? Do females of a particular kin-line show a tendency for a specific behaviors? One hypothesis of this study is that there are kin-specific patterns of behavior in the between-mount intervals of mount sequences. In order to test the relationship between kinship and behavior in the context of between-mount intervals, it is necessary to compare the frequency with which related females vocalized, and the frequency of occurrence of specific call types, against the frequencies of other kin-related females.

Age

Ontogenetic differences in behavior are pervasive in non-human primate species. Learning is a key factor in the development of social behavior. With respect to vocal behavior, animals must learn the appropriate context for different vocalizations (Cheney and Seyfarth, 1980). Green (1981) points out in his article on sex differences and age gradation in Japanese macaque vocal behavior there is evidence for differences in

age-class specific use of certain calls, e.g. the use of "roars" by adult males. The work by McDonald (1983) suggests that females of different ages exhibit different patterns of solicitation behaviors. Are there age differences in the frequency of behaviors exhibited by females in between mount intervals? Researchers who have studied Japanese macaques during the breeding season express the opinion that young females generally vocalize more than older females (Gouzoules per. comm). The behavior of vocal advertisement is characteristic of younger females. Do younger females employ characteristic patterns of vocal behavior during mating as well? An important hypothesis of this study is that there are age differences in the pattern of prompting in between mount intervals. In general, then, the sociological variable age is hypothesized to be associated with differences in behavior.

Parity

Parity (a measure of the number of infants a female has produced) is normally divided into three general categories: nulliparous, primiparous, and multiparous. However, within these categories there are possible gradations, e.g. multiparous females can be grouped on the basis of total number of offspring produced. A female's parity is a general indicator of her maternal experience. Parity can also be a measure of mating experience or more strongly put, a measure of successful mating experience. Parity does not correspond exactly with age, e.g. one nine year old female might never have had an infant while others of the same age might have had between one and four offspring. A nine year old female who has had three infants can be said to have been more successful at mating than a female of the same age who has had fewer or no infants. (Mating success should not be confused with the notion of reproductive success. The former is an expression of short term success, while the latter, which takes into account infant survival, is an expression of long term success).

Studies of maternal behavior have demonstrated that more experienced females exhibit different patterns of behavior towards their infants than do neophytes (Gouzoules, 1980). Are there differences in patterns of behavior exhibited by females of different parity in the context of mating? Do experienced, successful maters behave differently than experienced yet unsuccessful maters? It is hypothesized that parity will influence the

behavior of females in between mount intervals.

Maternal Status

Longitudinal studies of reproduction in Japanese macaques suggest that females have a two year cycle, related to inter-birth interval (Fedigan and Gouzoules, 1978) Thus, on the average, females have an infant every two years. During the breeding season, females with an infant from the previous birth season come into estrus later, have fewer and shorter estrus periods, have fewer consorts, and generally have less active breeding seasons (Takahata, 1980). Females without infants, on the other hand, have a greater number of consorts (including homosexual consorts) and generally tend to be very active (Fedigan and Gouzoules, 1978).

One explanation for this phenomenon is that lactation tends to supress ovulation and consequently the intensity of the estrous cycle (Small, 1982). It is also possible that the physical presence of an infant is a hinderance to the female, especially when pursuing a male. As well, because females with infants are known to be nervous and protective around adult males, the presence of an infant may deter a male from approaching an estrous female. In general, females with infants are more subdued through the breeding season. Do females with infants from the previous breeding season show differences in their behavior during mating bouts from females without infants? If a lactating female's estrous is less intense does she exhibit behaviors less frequently? Maternal status is hypothesized to influence patterns of behavior in between-mount intervals.

H. Contextual Variables

As discussed earlier, patterns of estrous female communicative behavior may be influenced by contextual factors as well. In this study, both the age-class of the male partner and the duration of intervals between the mounts in a mating bout will be investigated with respect to their potential influence on the communicative behaviors exhibited by females.

Partner Age-class

Throughout the breeding season, females establish consorts with males of varying ages. Males can be divided into three age-classes; juveniles or pubescent males, sub-adult males, and adult males. Pubescent males may not have reached spermatogenesis, and will have participated only minimally in previous breeding activities. Sub-adult males, while sexually mature, have not fully developed physically, nor do they fulfill the social roles of adult males (Fedigan, 1974). Adult males are both sexually and physically mature (see Chapter 3 for further discussion of this point).

Studies of the sexual behavior of males indicate that patterns of courtship and mating are learned behaviors (Eaton, 1978; Hanby and Brown, 1974; Nigi et al, 1980; Rostal and Eaton, 1982; Wolfe, 1979). Recently, Rostal and Eaton (1982) demonstrated the while younger males did show the ejaculatory response during mating, the appearance of adult patterns of behavior did not appear until several years later. The researchers also showed that younger males had fewer ejaculations and fewer partners during the breeding season than did adult males. Gouzoules et al. (1983) argue that younger males are more likely to be disrupted during mating than are older males. Hanby and Brown (1974) found that younger males required more mounts to ejaculate than older males. The sexual activities of inexperienced males are often comical to observe. Since mating is a learned behavior, young males very often make "mistakes': they often fail to mount properly and thus fail to reach intromission. The overall pattern of mounting is very erratic as well. The above findings indicate that there is considerable variation with respect to male mating behavior.

Given that males of different age-classes exhibit differences in mating, it can be hypothesized that females will respond differently with partners of differing ages. Support for this hypothesis come from the studies on female communicative behavior during mating described above (Michael and Zumpe, 1970; Zumpe and Michael, 1977). As mentioned earlier, these studies showed that females employed different frequencies of behaviors with different male partners. Do females generally prompt more with young males? It is hypothesized that partner age-class will affect female behavior during between-mount intervals.

Interval Duration

The issue of the duration of between-mount intervals in a mating bout is an integral, yet poorly examined aspect of series mounting in macaque species. The importance of interval duration in influencing female behavior requires an understanding of the physiological aspect of series mounting. The origin and function of series mounting are not entirely understood, yet the issue of series mounting is of interest to primatologists because of its relatively limited distribution throughout the primate taxa. Interestingly, as Fedigan (1982) and others (Michael and Zumpe, 1971; Saayman 1970) have noted,

> with few exceptions, the species which copulate through series-mounting also exhibit...[the] sociosexual pattern known as "consorting" and those which single-mount generally do not (Fedigan, 1982; p 141).

The exact physiological effects of series mounting are not fully understood, however, it is generally held that

> the repeated intromissions initiate a neuro-endocrine reflex which leads to the secretion of the progesterone (in females) in amounts sufficient to induce implantation and successful pregnancy (Alder, 1969, p.614).

The majority of information on the physiological effects of series mounting comes from studies of rodent species (Adler, 1969; Adler et al., 1970; Dewsbury, 1981). Adler (1969) concludes that series mounting serves two main functions: first, multiple intromissions induce hormonal conditions in the female which facilitate implantation of the ovum, and second, multiple intromissions facillitate transport of the sperm through the cervix. A study by Chester and Zuker (1970) on series mounting in rodents concurs with the above researchers with respect to the transport of sperm. In their study, they found that at a very minimum, 3 mounts with intromission were required in order to ensure impregnation of the female, and the optimal number of intromissions was between 9 and 16. Bermant (1964) investigated the effects of the number and timing of multiple intromissions. He concluded that, for the female, stimulation from an intromission decayed more quickly than for males, suggesting two competing systems. (McClintock [1983] suggests that in domestic strains the situation is reversed.) Bermant argues that females prefer a shorter interval between mounts to ensure maximum buildup of stimulation prior to male ejaculation. For the male, on the other hand, the stimulation from intromissions lasts longer and and males thus prefer a longer between-mount interval.

The resulting pattern of mounting is thus seen as a compromise between the needs of the female for short intervals and those of the male for longer intervals. Krieger et al. (1976) argue that:

> one must reach the conclusion that the observed sequence of copulatory events in the rodent is an interaction of the behavior of the male and the female rather than a function of one partner or another (p 386).

The work by Edmonds et al. (1972) suggests that differences in stimulatory effect of intromissions may account for the patterning of mating bouts, but they argue that it is ultimately the number of intromissions received by the female which determines successful impregnation. Their experiments

> demonstrate that multiple intromissions can, in some cases be adequate stimuli for the induction of the progestational state even if intervals as long as 4 hours are imposed between blocks of intromissions or if intervals as long as 60 min are enforced between individual intromissions (p 163).

This is provided, of course, that a minimum number of intromissions have been completed before the interruption. (A minimum of 10 in their study.)

There is considerable evidence from the rodent literature which suggests that the behaviors exhibited by females during a mating bout are directly related to the timing of mounts in a series (Doty, 1974; Krieger et al., 1976; McClintock et al., 1978; McClintock 1981). These studies indicate that females develop strategies which function to regulate the intervals at which they receive mounts, at the same time ensuring the optimal number of mounts necessary to ensure sucessful implantation. In McClintock's (1982) study, females employed avoidance strategies which appeared to maximize the optimal interval rate.

To date, studies of series mounting in non-human primates have ignored the duration of intervals between mounts, concentrating instead on the number of mounts and/or ejaculations received by a female. However, as has already been pointed out, these studies have failed to account for variation in female behavior during the mating bout. Rodent studies have shown a relationship between female behaviors and the timing of mounts. Given that Japanese macaques are series mounters, by analogy it is possible to hypothesize that female macaque behaviors are related to between-mount interval duration as well.

In the case of Japanese macaque mating, disruptions and delays can occur, lengthening the duration of the interval between mounts. As well, it has been shown that

in consorts with younger males the patterning of mounts in a series is erratic. Since there is some evidence that females exhibit behaviors to control the timing of interactions, i.e. they prompt the male, is it possible that female demonstrate more of these behaviors in longer invervals? Does the frequency of prompting behaviors, both vocal and non-vocal, increase with the length of the interval? It is an important hypothesis of this study that the timing of mounts in a series is a key factor in influencing female behavior.

III. Methods

A. Study

Data for this study were collected from the end of September to mid-December, 1981, coinciding with the major portion of the breeding season. The study began in the very early stages of the season (only three brief consorts had been observed prior to this study) and terminated several weeks after the peak of the mating season. Data collection was preceded by a three week visit to the study site during the birth season in May-June of 1981. This first visit served to familiarize the observer with both the study troop and field conditions.

Study Troop

This study involved observation of the semi-free ranging Japanese macaque troop at the Arashiyama West Institute (A.W.I.) in Dilley, Texas. The monkeys at A.W.I. originate from the mountains near Kyoto, Japan.

The Arashiyama monkeys have been studied by Japanese primatolgists since the early 1950's. Continuous geneaological data has been kept on all monkeys since birth. Due to the technique of supplemental provisioning of animals to facilitate observation, the population grew rapidly, culminating in a fissioning of the group in 1966 (Koyama, 1966). The pressures of two groups in the area, combined with the expansion of the suburbs of Kyoto into the area, created serious competition for space. The Arashiyama A group was caught between the B group and the encroaching suburbs. Members of the A group began forays into the suburbs, raiding gardens and garbage, eventually becoming a serious nuisance. A new home was sought for the Arashiyama A group; one which would enable them to remain as a cohesive social unit and ensure continued accumulation of data on the troop. In February, 1972 the entire Arashiyama A troop, (renamed Arashiyama West), along with a small group of peripheral males associated with the troop, were transplanted to a ranch 30 miles north of Laredo, Texas. A subsequent move to a ranch near Dilley,

Texas took place in August 1979.

A.W.I. maintains comprehensive geneaological and life history data on every individual troop member. Researchers have easy access to the precise information about animals; who their kin are, how many infants they have had, how old they are, etc. An additional advantage of working with the A.W.I. monkeys is that it is possible to identify every individual within the troop. A system of facial tattoos, small dots on the face which correspond to different numerical values, enables the researcher to quickly and accurately identify individual animals. The availability of accurate data about all individuals in a troop allow specific questions to be asked about the influence of sociological variables on behavior.

Study Site

The Arashiyama West Institute is situated on a large ranch, approximately 15 miles from Dilley, Texas; 60 miles south of San Antonio. The monkeys are kept in a 50 acre enclosure, surrounded by an electrified fence. The fence acts as a general deterrent to the troop, although young males, who typically emigrate from their natal troop, are not hindered by the fence.

Running through the enclosure is a shallow ravine, vegetated by plant species common in the area; predominantly acacia (Acacia sp.), mesquite (Prosopsis sp.) and tall Bromus grasses. In the ravine there are two man-made reservoirs which support many large acacias. On either side of the ravine are cultivated fields which are cleared annually and planted with wheat. Man-made structures for shade and climbing are distributed throughout the enclosure.

The animals range freely within the enclosure, foraging on the available food resources. Once a day, the animals are provisioned with maize and/or milo, Purina monkey chow or cattle pellets, and various types of vegetable produce. Peanuts and watermelon provide seasonal variation to the diet.

There are no large predators, eg. coyotes or bobcats, within the enclosure. Raptors hunt within the enclosure, but are thought to pose no threat. The only real danger is posed by rattle snakes, one of several species of snake found within the enclosure.

Study Population

According to the 1981 census, the A.W.I. troop consisted of 275 animals. Of these, 114 (41%) were immature juveniles 1.5 to 2.5 years old (63) and 1981 infants (51). Juveniles and infants were not included in the study population. The remaining 161 troop members (representing 59% of the entire population) were all considered to be potential participants in the breeding season and thus constitute the study population.

Although there is some variability with respect to age of onset of sexual maturation, the norm is reported at approximately 4.5 years (Hanby, 1971; Nigi et al., 1980). However, even if the 3.5 year olds are not sexually mature, they often do begin to participate in the breeding season, i.e. they form consorts. Therefore, the study population includes all individuals 3.5 years and older.

Of the 161 animals in the study population, 68 were males (40%) and 103 were females (60%). Males are classified into age-classes accordingly; pubescent males (3.5 - 4.5), subadult males (5.5 - 8.5), and adult males (9.5 and older). The 103 females in the study population were first categorized on the basis of parity. There were 32 nulliparous, 11 primiparous and 60 multiparous females in the study population. The nulliparous category was originally divided into three subgroups: first estrus or pubescent (3.5 -4.5), nulliparous (5.5 - 6.5), and old nulliparous (7.5 and older). Old nulliparous females represent an unusual and small group. These females are older than the average age of a female at first birth, 5.5 years, and have still not had an infant. Of the 103 females, 32 have not had an infant (31%). The remaining 71 females have had at least one infant (69%). Those females who had at least one infant were grouped on the basis of their 1981 maternal status; those with and those without an infant from the preceeding birth season. The three females whose infants died neonatally (for the purposes of this study infant deaths within the first 6 months) were included in the without-infant category.

B. Sample

An attempt was made to collect equal amounts of data on equivalent numbers of females from each of the 9 categories outlined above. Table 2 shows a breakdown of the study sample, consisting of 25 females and 55 male partners. A list of 'potential' subjects within each category was compiled, from which a list of 'preferred' females were selected for each category. On any given day, an attempt was made to locate the 'preferred' animals. If a preferred animal was observed in estrus, in the context of pursuing a partner or in consort with a partner, data were collected on that individual. Then, a scan to locate other females from the list was conducted. In scanning for preferred animals, priority was given to locating those females for whom the least amount of data had been collected. If, after a scan, the list of preferred females was exhausted, data were collected on other females from the list of potential subjects.

Several factors tended to interfere with sampling. First, not all categories were equally represented within the study population. Consequently, certain categories had a higher probability of being observed than others. A case in point is the 'primiparous without-infant' category. This category contained only three individuals (2% of the study population) as compared to first-estrus females which numbered 22 individuals (13% of the population). To complicate matters even further, one of the three 'primiparous without-infant' females died during the breeding season, further reducing this already small category.

The differential activity levels between the various categories of females is a second factor which influenced sampling. Although an attempt was made to collect data on females in estrus, in the specific context of mating, females were not equally likely to be consorting. As has already been mentioned, females with infants from the previous birth season have a less active breeding season than do females without infants. As well, old nulliparous females exhibit very infrequent sexual behavior. Conversely, young females and multiparous females without infants are very active throughout the season.

The differential observability of individuals complicated sampling as well. Lower ranking and/or less central animals are not as likely to be observed as a central troop member (Altmann, 1974; Drickerman, 1974). Pubescent females, for example, are very nervous and avoid adult males by remaining on the periphery of the troop. These females

Table 2 Study Sample Distribution (N=25 Females)

Variables	Groups	N	%
Kinship	Betta	4	16
	Matsu	6	24
	Rheus	5	20
	Pelka	3	12
	Nose	3	12
	Petitmon	3	12
	Other	1	4
Age	3 - 6	8	32
	7 - 10	9	36
	>10	8	32
Parity	Nulliparous	7	28
	Primiparous	6	24
	Multiparous	12	48
Matstat	With Infant	8	32
	No Infant	7	38
	Neonatal	3	12
	Other	7	28
Partner[1]	Adult	26	47
	Subadult	18	33
	Juvenile	11	20

1. N=55 male partners.

avoid the main troop, usually staying in densely vegetated areas where they are not easily observed. Walk-through scans, at regular intervals throughout the day, were designed to decrease the influence of all of these sampling problems.

C. Data Collection

Behavioral data were collected on each of the 25 females in the various contexts outlined above: vocal advertisement, female courtship, homosexual mating and heterosexual mating, totalling 150 hours. For the context under investigation, mating, a total of 45 hours of data were collected.

Focal Animal

Twenty-minute focal animal test sessions were taken on subject animals. The subject animal was identified along with the individuals with whom she interacted. Aside from noting the date and time of day, general contextual information such as weather conditions and location of the subject with respect to the central troop was also recorded. The major behaviors performed by or directed at the subject animal, as defined by an ethogram, were recorded along with notable contextual factors. The duration of behaviors was recorded using a stopwatch.

The ethogram, a list of discrete observable units of behavior, is a central tool of ethological research. As a research tool it is not without problems. The segmenting of discrete units from a continuous flow of behavior is admittedly an arbitrary process, however, its advantages far outweigh any artifacts it might produce. The ethogram employed in this study does not depart from traditional ethological conventions. The units identified in the ethogram are typically stereotyped, recurrent behaviors which I was able to recognize and record given the exigencies of data collection. The ethogram is in part a reflection of my observational skills as well as a reflection of Japanese macaque behavior.

The ethogram for this study was developed before going to the field from previous studies of Japanese macaques (Fedigan, 1974; Gouzoules, 1980; Stephenson, 1973). Refinements to the ethogram were made at the beginning of the study during the first weeks of general observation, prior to data collection. All behaviors are unique.

Behaviours can be divided into states and events. States are ordered hierarchically and are mutually exclusive. Some events trigger a change in states (state-breaking events) while other events occur during states, often in conjunction with other behaviors.

Following is the list of units of behaviors (and their definitions) employed in this study:

States

States are behaviors of a durational nature, i.e. behaviors that are ongoing (Lehner, 1979). States are arranged hierarchically and are mutually exclusive. Onset time of each state is recorded throughout the session.

1)*Follow* (fol); Animal moves in same direction as preceding animal, continually monitoring progress of animal; may keep some distance back, stopping when animal stops, etc.

2)*Flee* (fle); Animal moves rapidly away from another animal. (More active and sustained than leave).

3)*Forage* (for); Animal actively searching for and eating food. Animal may be sitting, standing or moving slowly.

4)*Locomote* (loc); Quadrupedal locomoting climbing etc.

5)*Groom* (gro); One animal grooms another.

6)*Self-groom* (seg); Animal grooms self for extended duration (scratching not scored).

7)*Sit* (sit); A general inactive category; includes resting, observing, etc. (posture not relevant).

Events

Events are behaviors of a rapid or transitory nature (Lehner, 1979). Events may be repeated consecutively, and can occur within states in conjunction with other behaviors. May be directed or received by animal. Events in the etogram starred by an asterisk (*) are of intermediary duration and usually indicate a transition from one state to another.

8)**Leave* (lea); Animal moves away from other (occurs with loc or fle).

9)**Approach* (app); Animal moves within close proximity of an other animal.

10)*_Sit Against_ (sia); Animal, with legs apart, sits up against the haunches of an other animal.

11)*_Sit Beside_ (sib); Involves some type of gross body contact.

12)*_Sit Near_ (sin); No body contact but in proximity to the other animal.

13)_Threat_ (thr); Type of threat; stare, lid, jaw, to be recorded in comments. Can occur with threat vocalization.

14)_Lunge_ (lun); Lunge at but no contact with animal.

15)*_Chase_ (cha); Violent charge and active pursual of animal.

16)_Pin and Bite_ (pab); Animal holds down other animal and bites (often repeatedly).

17)_Bite_ (bit); Animal bites or attempts to bite other animal without pinning other animal.

18)_Fear Grimace_(feg); Lips retracted from teeth, teeth clenched.

19)_Lip Quiver_ (lip); Rapid movement of pouted lips.

20)_Hip Touch_ (hip); A touch or pull on the pelvic area of another, a precursor to mounting.

21)_Attempt Mount_ (atm); Unsuccessful attempt to mount.

22)*_Mount_ (mou); Mount without pelvic motion of mounter. Type of mount position specified in comments if other than double-foot clasp mount.

23)*_Mount-thrust_ (mot); Mount with noticeable horizontal pelvic thrusts.

24)*_Mount-rub_ (mor); A typical female-mount position with rubbing; less jerky than thrust.

25)*_Mount-ejaculation_ (moj); Ejaculatory pause in thrust sequence. Often accompanied by noticeable ejaculate.

26)_Gaze_ (gaz); Prolonged staring, usually at face of other.

27)_Turn and Look_ (tul); Animal turns head and looks at consort partner.

28)_Look Down_ (lod); Mounting animal lowers head to head of other animal during mount.

29)_Look Back_ (lob); Animal looks over shoulder to face mounter.

30)_Reach Back_ (reb); Animal reaches back and grabs pelage on chest or arm of mounter (can occur with lob).

31)_Food Call_ (fod); A characteristic vocalization very prolonged, given just prior to

feeding or with arrival of feeding truck.

32)*Vocalize* (voc); Includes all vocalizations other than food call. Can occur with other events or independently (see discussion below).

33)**Infant Nipple Contact* (nip); Infant may or may not be nursing.

34)**Infant Ventral Contact* (ven); Infant clings to ventrum or sits in lap.

35)**Infant Gross Body Contact* (bod); Contact other than ventral.

36)*Punish Infant* (pun); mother prevents infant from contact, includes pinch, stare, push

37)*Retrieve Infant* (ret); Mother grabs infant and initiates clinging.

38)**Carry Infant* (car); Occurs with any form of locomotion. comments indicate ventral or dorsal.

39)*Present for Mount* (pfm); Female stands, raising haunches off ground.

The following behaviors were originally recorded in the comments section and were later incorporated into the ethogram.

40)**Lead* (led); walking ahead of, while monitoring, other animal. Animal may respond to changes in direction, etc. of "follower".

41)**Stand Beside* (stb); Stand near animal after dismount before returning to sitting position.

42) *Slap Ground* (ground); hitting ground with open palm

43)*Manipulate Object* (obj); Manipulating branch or nearby object; usually with one hand.

44)*Shudder* (shud); Small jerks or convulsions, similar to those given with gecker vocalizations.

D. Recordings

Recordings of vocalizations were made on a Sony cassette tape recorder (model TC-D5) using a Sony stereo condenser microphone (model ECM-990F) on cromium dioxide tape. The audio recordings were intended for structural analysis of the vocalizations. Originally, attempts were made to record a female while collecting focal animal data, however, this procedure proved unsatisfactory. Animals are highly mobile often moving quickly through thick brush. Trying to manoeuvre through the brush while still managing to record focal animal data, without the audio equipment getting caught up in the branches, was a skill this observer never successfully mastered. Instead, audio recordings of estrus femaless were collected independently to supplement the focal animal data. Contextual notes were taken during audio recordings. The audio recordings were taken on an ad libitum, opportunistic basis.

Vocalizations

Each instance and type of vocalization was recorded for each focal animal session. In order to classify vocalizations: 1) reference was made to descriptions of vocalizations from previous studies of Japanese macaques (Itani, 1963; Green, 1975) and, 2) a sample of different vocalizations was collected at the beginning of the study and sent to an acoustic phonetics lab for preliminary spectral analysis. The following vocalization categories were originally identified for use in this study:

1)*Hack*: (see sonagram; Fig. 2, Chapter 4);

A single component vocalization impressionistically similar to a sin single component of the gecker vocalization.

2)*Gecker*: (see sonagram; Fig. 4, Chapter 4)

A stacatto vocalization comprising a series of components repeated in close succession. Geckers have been described in the literature with respect to a) estrous females and b) infant or juvenile weaning tantrums. The vocalization is often accompanied by convulsive jerking.

3)*Scream*: (see sonagram; Fig. 6, Chapter 4)

A single component vocalization of high intensity and long duration given a) in agonistic interactions and b) by estrus females.

4)*Defensive Scream*: (see sonagram; Fig. 9, Chapter 4)

A scream accompanied by submissive behaviors. The animal often defecates and/or urinates.

5)*Contact Call*:

Short, low amplitude vocalization. May be produced singly or in a series.The contact call is a low intensity vocalization and is given frequently at dusk as the animals group together. It is also given when foraging in tall grass. Often given by estrous females when a partner leaves during a mating bout.

6)*Coo Call*:

Similar to contact call but of long duration. A variable class of vocalization (Green 1975). Employed by estrous females in pre-consort solicitation or when consort partner remains away for extended period.

7)*Social Approach*:

A low intensity vocalization uttered singly or in succession. Given as an animal approaches or approaches in close proximity to a dominant animal. Often accompanied by submissive gestures.

8)*Threat*:

A stacatto, noisey vocalization composed of a series of repeated components. An intense vocalization, used in agonistic interactions between individuals. Given by estrous females after being chased by a male.

9)*Alarm*:

A single or multiple component vocalization, given in contexts of surprise, such as an audible explosion from seismic crews or a low flying crane.

In many instances two different vocalizations were given in conjunction, creating a composite vocalization. These vocalizations were labelled with respect to their recognizable component parts. The four major composite vocalizations were: a)Prolonged Gecker, b)Scream/Gecker, c)Contact/Gecker and d)Contact/Scream.

E. Hypotheses

Following are the hypotheses to be tested concerning variation in the behaviors of females during between-mount intervals:

(1) Rates of prompting behavior will differ significantly between groups of related females.

(2) Higher rates of vocalization will be associated with younger females.

(4) Higher rates of non-vocal behavior will be associated with older females.

(5)Rates of prompting behavior will differ significantly between parity classes.

(6)Rates of prompting behavior will differ significantly between females with and females without 1981 infants.

(7)Rates of prompting behavior will be significantly different for consorts involving adult and sub-adult male partners.

(8)Higher rates of prompting behaviors will be associated with between mount intervals of longer duration.

F. Data Analysis

Behavioral Data

The data used for analysis were taken from focal animal tests. Written information from data sheets was transformed into a numerically coded system and then entered on the computer. Given the fact that females did not mate with equally as often, an attempt was made to equalize the sample. Data from a minimum of two (2) and a maximum of three (3) consorts per female were analyzed.

The data were comprised of mating sequences isolated from focal animal sessions. The beginning of a mating sequence was defined as the first mount or between-mount interval for which the onset time could be determined. This controlled for those focal animal tests which began in mid-context. A mating sequence was said to have ended if a) the focal animal test ended, b) mating behaviors stopped, i.e. the animals stopped mounting and no pursual behavior was observed, or c) the time after the last

recorded mount exceeded five minutes, even though the animals continued exhibiting pursual behavior. In the latter case, it was felt that intervals which involved prolonged pursuals were different in nature than those in which the animals reestablished mating after an interruption (Hanby, 1972).

Using the SPSS program (Statistical Package for the Social Sciences [Nie et.al. 1975]) descriptive statistics were obtained for the mating sequences comprising the sample. Results are summarized in Table 3. The sample consisted of 55 consorts or mating bouts. The mean bout duration was 1004 seconds and the modal duration was 1200 seconds (20 minutes). Within these consorts, there were 741 between-mount intervals for which total duration was known. Figure 1 shows the distribution of the 741 intervals with respect to duration. The mean interval duration was 46.9 seconds, and the modal interval was 27 seconds. Finally, the mean number of intervals and the mean interval duration was determined for the sample, based on the mean number of intervals and the mean interval duration of each of the 25 females (Table 3).

Vocal and non-vocal behaviors were grouped and rates of occurrence were calculated for each category. Rates were computed by dividing the total number of occurrences of a given behavioral category by the duration (in seconds) of the interval in which they occurred. A mean rate, i.e. the number of behaviors per 10 seconds, was calculated for each of the females.

The behavioral categories are as follows:

Non-vocal:

1. Attempt-mount (ATM) or Mount-rub (MOR)
2. Turn-and-look (TUL)
3. Other (Present-for-mount, Slap-ground, Manipulate-object)

Vocal:

1. Hack
2. Gecker
3. Prolonged Gecker
4. Scream/Gecker
5. Scream
6. Compounded Contact

Table 3 Descriptive Statistics of Mating Bouts

	N	Mean	S.D.	Mode	Kurtosis	Skew
Bout Duration (for sample)	55	1004.0sec	539.5	1200	1.05	0.98
Interval Duration (for sample)	741	46.9sec	50.6	27	32.30	4.82
Mean # of Intervals (per subject)	25	29.6	17.0	14	0.41	0.61
Mean Interval Duration (per subject)	25	49.4sec	17.4	53	3.67	1.44

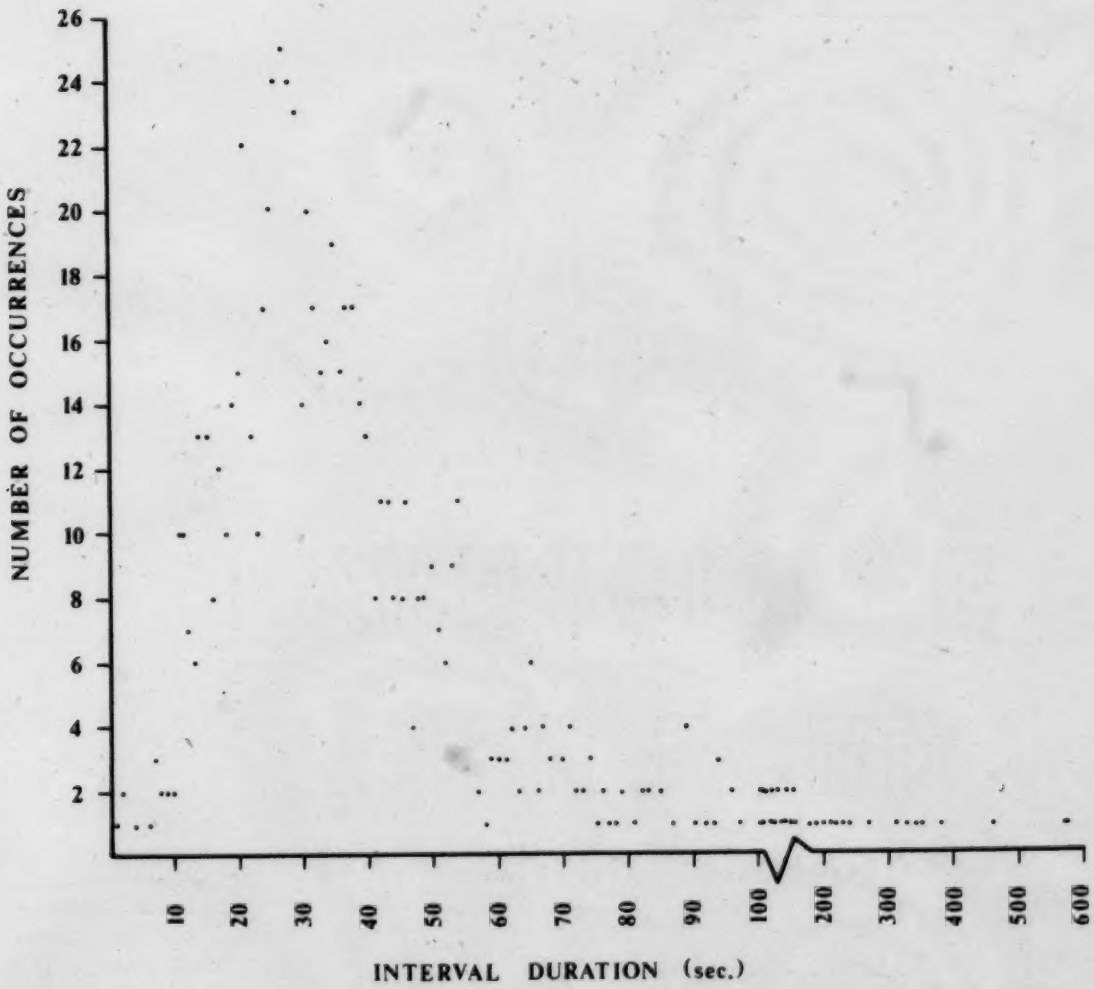


Fig 1. Distribution of Between-mount Interval Durations

7. Defensive Scream
8. Contact
9. Other (Social Approach, Coo, Threat, Alarm)

Table 4 shows the mean rate of occurrence for each category for the entire sample of 25 females.

Statistical Tests

The potential for skewness in the data necessitated the use of non-parametric statistical tests for differences in rates of behaviors between the various subgroupings of females. Tests of association, involving variables of a continuous nature, i.e. age and interval duration were tested using the Spearman's Correlation statistic. Variables of a Differences between females were tested using the Kruskal-Wallis statistic, for those variables comprised of more than two categories (parity and kinship). The Student's T statisitc was used to test for differences between two groups (maternal status and partner age-class).

Acoustical Data

Acoustical analysis was performed on a sample of each call type identified in the ethogram. Representative calls were selected for analysis on the basis of quality of the recording (i.e. those with low ambient noise). An attempt was made to record vocalizing animals within a 5 to 10 meter range, however, movement by animals during recordings was sufficient to warrant caution in comparing the overall amplitude of the different calls.

Sonagrams were made of each of the representative calls. For the most part, broad band sonagrams of each call were made over the 80 to 8,000 Hz range. The broad band filter has a frequency window of 300 Hz and averages adjacent harmonics, permitting an analysis of concentrations of energy throughout the spectrum. A 500 KC calibration tone conveniently marked the spectrum at 500 Hz intervals in order to facilitate the measurement of sonagrams. Given the persistence of low level extraneous noise throughout the recordings, the Automatic Gain Control (AGC) was set at zero, thus concentrating the analysis on the upper 32 dB of the signal.

Table 4 Rates (per 10 seconds) of Prompting Behaviors

Behaviors	Frequency Mean	S.D.	Occurence % of Pop
ATM/MOR	.003	.007	16%
TUL	.035	.036	84%
OTHER (Non-vocal)	.014	.031	40%
TOTAL	.053	.049	88%
HACK	.013	.034	24%
GECKER	.032	.049	60%
PROLONGED GECKER	.005	.013	24%
SCREAM/ GECKER	.001	.004	8%
SCREAM	.016	.053	34%
COMPOUNDED CONTACT	.001	.004	16%
DEFENSIVE SCREAM	.001	.002	32%
CONTACT	.005	.010	28%
OTHER (Vocal)	.002	.004	32%
TOTAL	.073	.133	68%
TOTAL PROMPT	.126	.136	92%

In the case of Scream vocalizations, which have elaborate harmonic structure, (ie. high energy at most harmonics throughout the spectrum) narrow band filter sonagrams were made to supplement the analysis. The narrow band filter has a smaller frequency window (45 Hz) which permits better resolution of individual harmonics. Finally, spectral sections of the three major vocalizations, Hack, Gecker, and Scream were made for comparison of energy distribution throughout the spectrum.

The mean measurements for each call type were determined using a grid overlay for the following variables:

1. Duration.

Calls of a single unit were measured from the onset to offset of energy in the area of most concentrated energy. Following Deputte and Goustard (1980), calls composed of multiple units were measured both for unit duration and call duration (ie. the sum of the unit durations plus intervals). (See discussion of Gecker vocalization duration below).

2. Fundamental frequency.

The Fundamental frequency (Fo) was measured at onset. In the case of frequency modulation or change throughout the call, Fundamental was also measured at its highest and most stable point.

3. Spectral characteristics.

The location of harmonics, i.e. bands of concentrated energy in the spectra were measured. Noise present in the signal was qualitatively estimated, as was the degree of frequency modulation throughout the signal.

IV. Analysis and Results

A. Acoustic Analyses

Following is an acoustical description of each of the call types in the ethogram from analysis of the representative sonagrams.

Hacks

Hack vocalizations (Figure 2) are composed of single units of short duration (approximately 70 msec) with a low Fo between 100-300 Hz. The call shows abrupt onset/offset characteristics and there is no observable frequency change. Although bands of concentrated energy can be seen at approximately 1000 Hz intervals throughout the 80-8,000 Hz range,wide band noise represented by dense vertical striations throughout the unit tend to smear the harmonic structure. (The perceptual impression is akin to "creaky voice" in humans caused by mixed excitation of voicing and noise). This wide-band noise results in a relative leveling of the amplitude display (Figure 3; spectral section of a hack utterance): valleys between amplitude peaks tend to be filled in, resulting in a relatively flat spectrum.

The overall characteristics of the Hack call are similar to the "harsh calls" described by Brown (1982):

> Harsh calls ... are noisy atonal calls. Although the structure of the harsh calls may be harmonic, it is usually blurred by wide band noisy overlay (p 149).

Harsh calls are adapted for short range communication: they tend to maximize locatability while diminishing propagation distance (Wiley and Richards 1982).

Geckers

The Gecker vocalization (Figure 4) is composed of a series of units or components (a mean of 3.2 units per call) of short but variable duration (range 30 msec - 100 msec, a mean of 62 msec, N=17). Intervals between units in a call range from 120 msec to over 400 msec (a mean of 254 msec) and the average call length is approximately 820 msec.

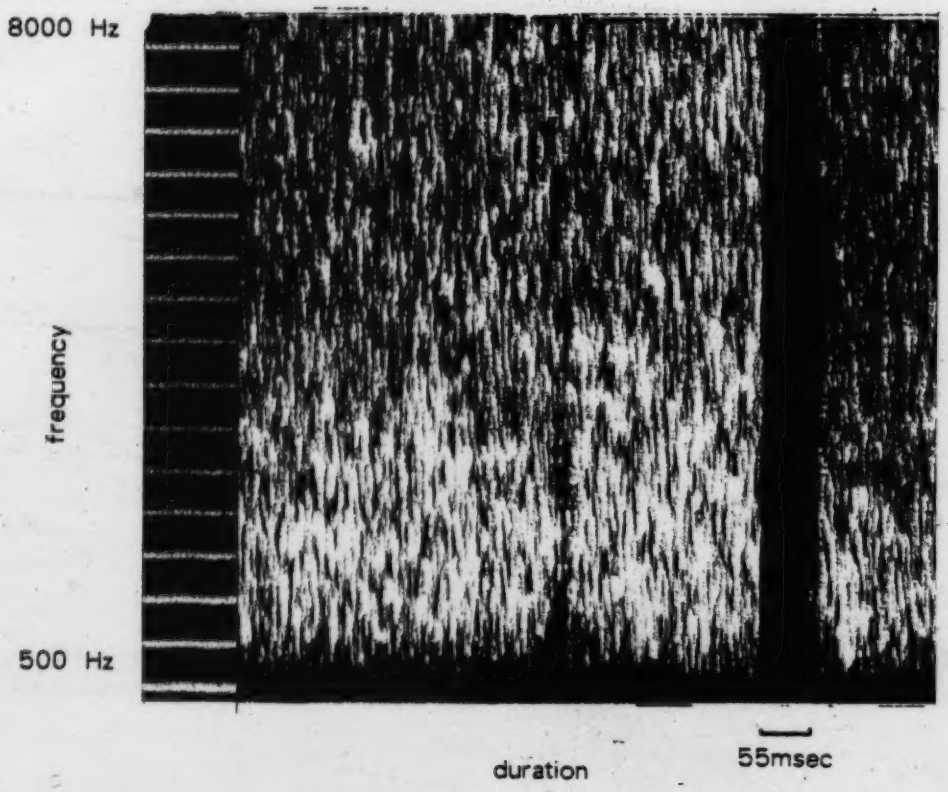


Fig 2. Wideband Sonagram of Hack Vocalization

Fig 3. Spectral Section of Hack Vocalization

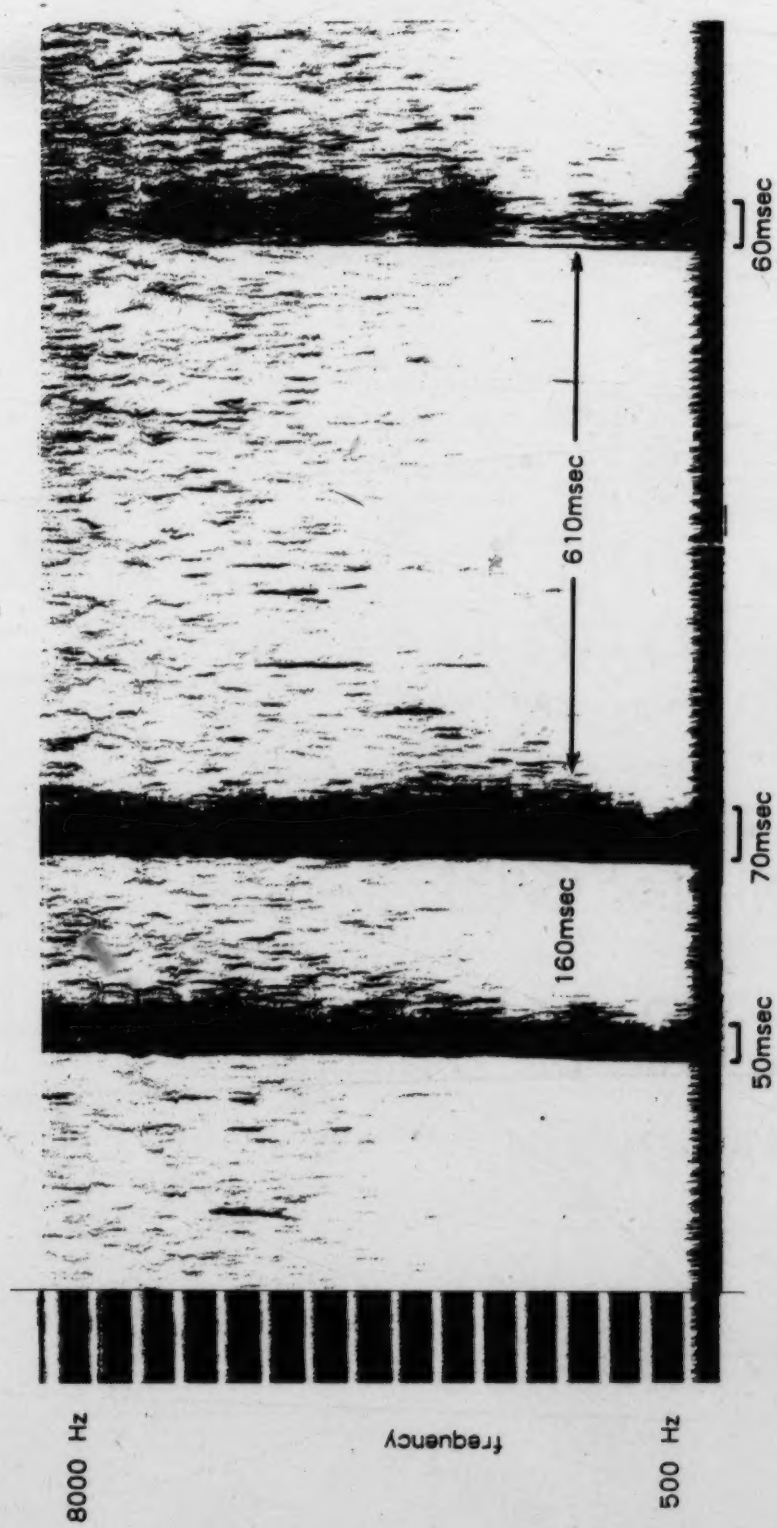


Fig. 4. Wideband Sonagram of Gecker Vocalization

Units at the end of a series appear to be shorter in duration and are separated by generally longer intervals, perhaps accounting for the variation in unit size and interval duration.

As with the Hack vocalization, the Fo of individual units in a Gecker vocalization is between 100 - 300 Hz. While there is no fundamental frequency change within a component, there is a tendency for the Fundamental to decrease over the duration of the call; final units in the vocalization tend to have the lowest Fo in a series. Reduction in the unit size, and Fundamental frequency may be the natural result of decreasing air pressure over time (Lieberman 1977). However, given the relatively low Fo of all Gecker units the decrease in Fo over the duration of the call is not substantial (cf. Screams below).

Bands of concentrated energy can be seen throughout the 80 - 8,000 Hz range, but, as with the case of Hacks above, wideband noise tends to obscure the harmonic structure. The degree of noise throughout Gecker units is impressionistically less than with Hacks, especially with final units in a Gecker series, however, the overall effect on the amplitude spectrum is the same (Figure 5), ie. valleys between peaks tend to be filled in.

Comparison of the acoustical characteristics of a single Gecker unit with a Hack unit reveals a close morphological similarity between the two calls. This close acoustical similarity between the two calls substantiates my own and other fieldworkers' perceptions of a strong similarity between the two calls (Green 1975; and Gouzoules, personal communication).

Successive repetition of Gecker units, possibly reflecting increased motivation, might slightly increase the propagation distance of the Gecker over the Hack, however, Geckers still do not reflect the characteristics of vocalizations adapted for long-distance propagation (Brown 1982, Wiley and Richards 1982). On the other hand, repetition of Gecker units would certainly improve the locatibility of the signal. Thus, it is still reasonable to argue that Geckers are primarily adapted for close range communication.

Screams

1. Simple Screams

Simple (as opposed to composite Screams dicussed below) Scream vocalizations are single unit calls of long duration; approximately 740 msec (range 460 msec - 1,000

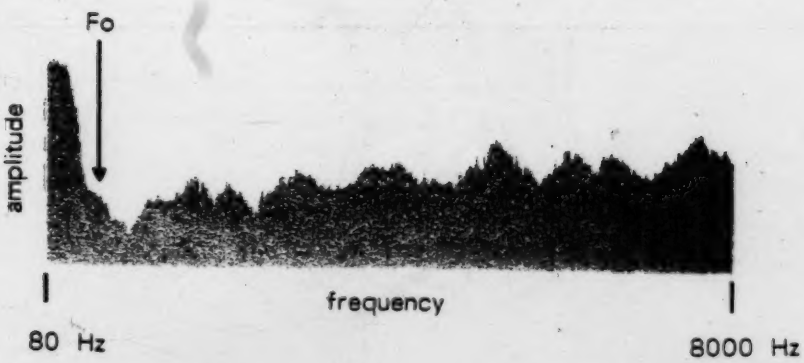


Fig 5. Spectral Section of Gecker Vocalization

msec, N=5) (Figure 6). The Fo of these calls is approximately 500 Hz at onset and are characterized by a rapid upward glide with the Fo reaching as high as 2,000 Hz. Although there is considerable frequency change throughout the duration of the call the Fo tends to be most stable at around 1,500 Hz. These calls generally end in a sudden downward sweep of all frequencies, perhaps due to closing of the mouth.

Harmonic structure is very well defined in Screams (Figure 7, narrow band sonagram) with energy equal to the fundamental concentrated in at lease three prominent harmonics. The amplitude display of Screams (Figure 8) shows an absence of energy at low frequencies, high peaks of energy between 1,500 Hz and 4,500 Hz, then a gradual diminishing of energy at higher frequencies. Noise striations appear at intervals throughout the call in vertical bands. The noise is nowhere as dense as in the case of Hacks or Geckers and combined with the fact that the noise is not continuous throughout the call the harmonic structure of the call is relatively preserved: valleys between amplitude peaks in the section are more pronounced than with either of the two call types described above.

There is an interesting anomaly associated with Screams that is not present in either of the other two calls; there is an abrupt change in the Fo, a jump of 300 - 500 Hz, which is assumed to be due to a "break" or discontinuity in the glottis during the uttering of the vocalization. Screams are very intense vocalizations and stress on the vocal chords may cause the voice to "crack".

Narrow band, harmonically structured calls with a marked intonation pattern or frequency change throughout the call are well adapted for long range propagation of sounds and are typical of the long range acoustic signals employed by both non-human primates (Brown 1982, Snowdan 1982) and birds (Wiley and Richards 1982). The Scream vocalization described above exhibits all of these characteristics, suggesting that the the propagation distance of Screams is greater than that of either Hacks or Geckers.

2. Defensive Screams

The Defensive Scream (Figure 9) is similar to the Simple Screams described above although it tends to be shorter (a mean of 350 msec) and may be uttered consecutively in a series. Defensive Screams exhibit the characteristic frequency sweep at onset, with frequency change and glottal disconinuities as well. The major difference between the

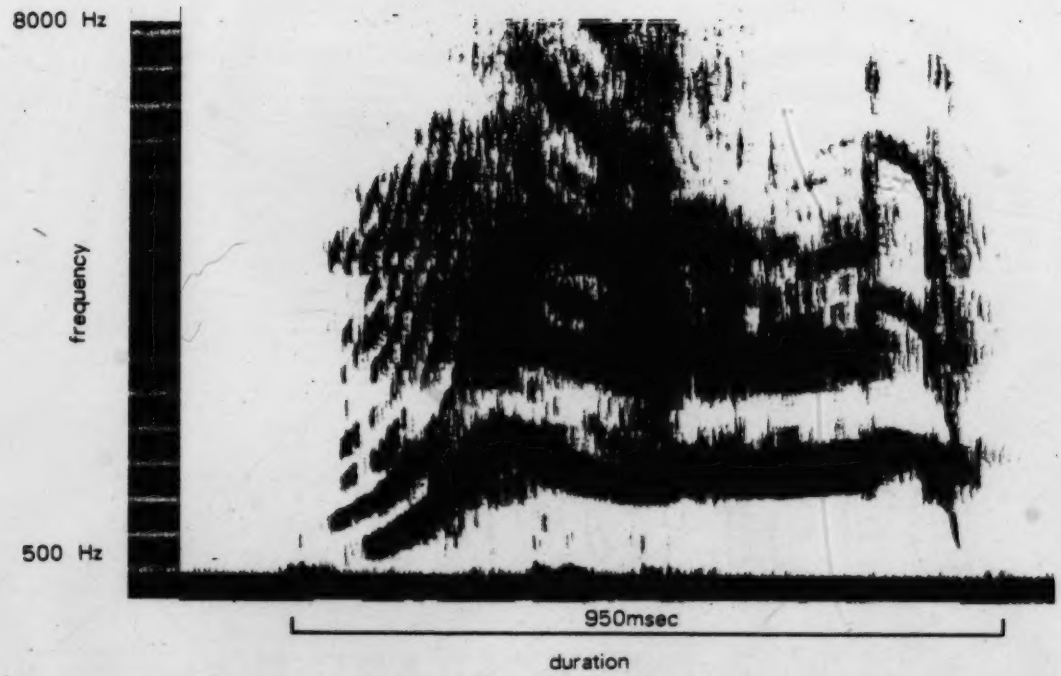


Fig 6. Wideband Sonagram of Simple Scream Vocalization

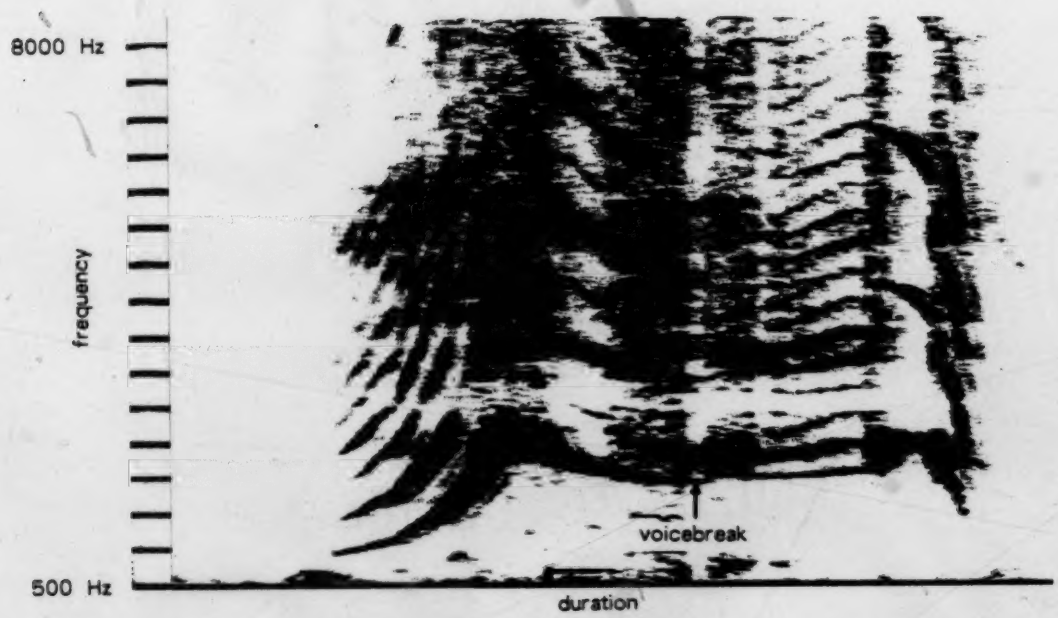


Fig 7. Narrowband Sonagram of Simple Scream Vocalization

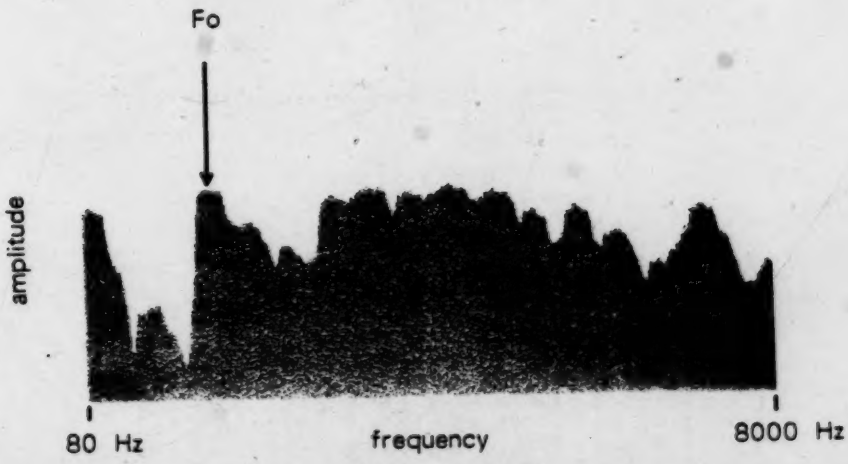


Fig 8. Spectral Section of Simple Scream Vocalization

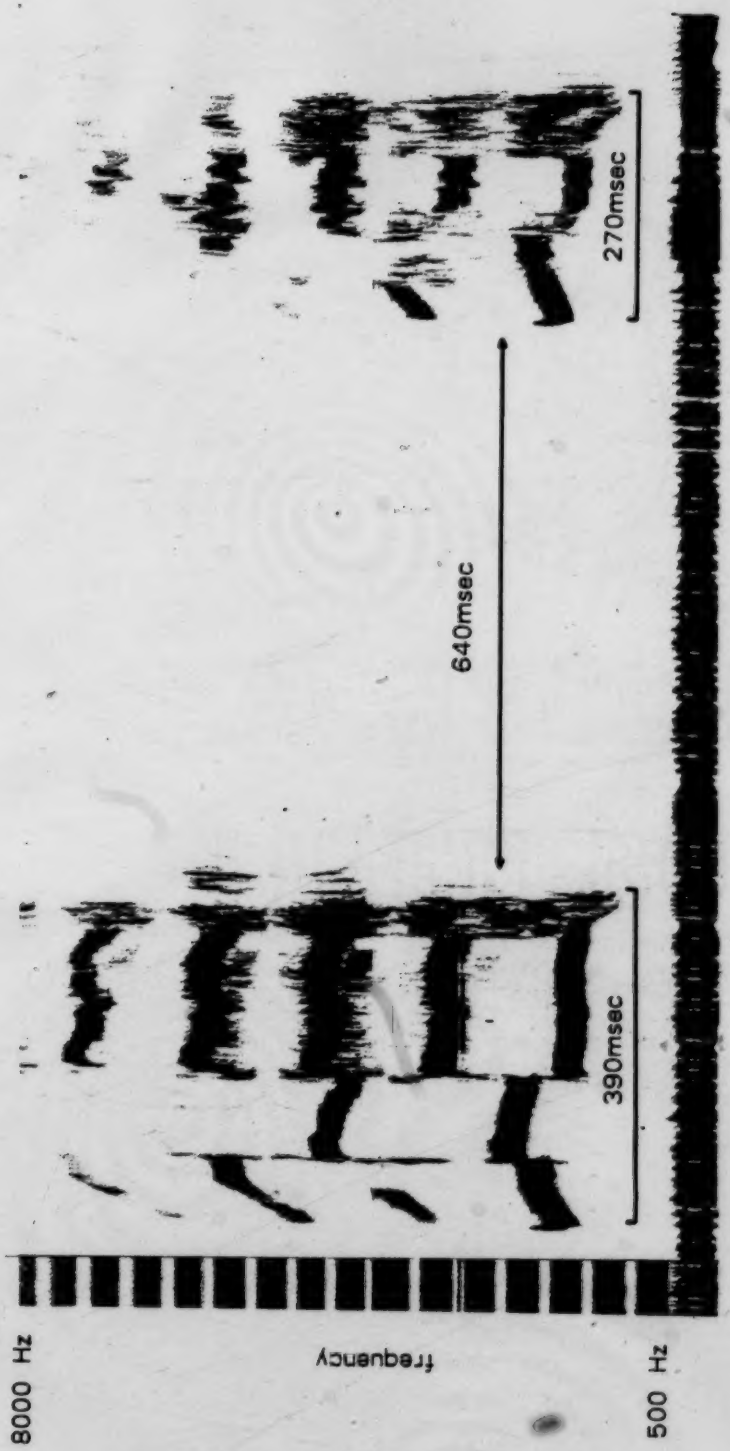


Fig 9. Wideband Sonagram of Defensive Scream Vocalization

two types of Screams is in their offset characteristics. The harmonic down-sweep associated with simple Screams is not as pronounced in the Defensive Scream and the harmonic structure is obscured by an overlay of broad band noise at the end of each unit. The down-glide in Simple Screams is attributed to closing of the mouth. The Defensive Scream, which is given by a consorting female during and following an attack by her partner or other male, is often associated with the characteristic fear grimace, in which case the vocalizing female might not close her mouth. Thus, the difference in the facial gesture or expression associated with the different types of screams could account for the observed acoustical differences at the end of the vocalizations. This difference in offset between Screams and Defensive Screams suggests a difference in motivational intensity; the mouth closing versus remaining open in a grimace. The difference would not, however, have a marked effect on the distance propagation of Defensive Screams.

3. Compound Screams

During the course of between mount intervals some females will produce a long series of vocalizations (this behavior is akin to weaning 'tantrums', during which time a juvenile will produce a protracted series of vocalizations starting with Geckers and ending in Screams). During focal animal recording sessions the identity of each vocalization type in a protracted vocal series was identified. At that time it was noted that females uttered some vocalizations which were perceived as a compounded Scream/Geckers or Gecker/Screams (depending on which vocalization came first). Examination of the sonagrams of these compound vocalizations reveals some interesting comparisons with simple Gecker and Scream vocalizations.

a) Scream/Geckers

Scream/Geckers are typically long duration, multiple unit vocalizations (Figure 10). The first components in the series are similar to Simple Screams; they have well defined harmonic structure, and they show considerable frequency change throughout the unit. However, the scream unit in the Scream/Gecker is much shorter in duration than a Simple Scream (a mean of 200 msec). These units also show abrupt onset rather than the frequency glide associated with Simple Screams. As well, the Scream unit of a Scream/Gecker vocalization has a generally lower Fo which is stable around 1000 Hz versus 1,500 Hz for a Simple Scream. (Fo at onset is about 500 Hz for both types).

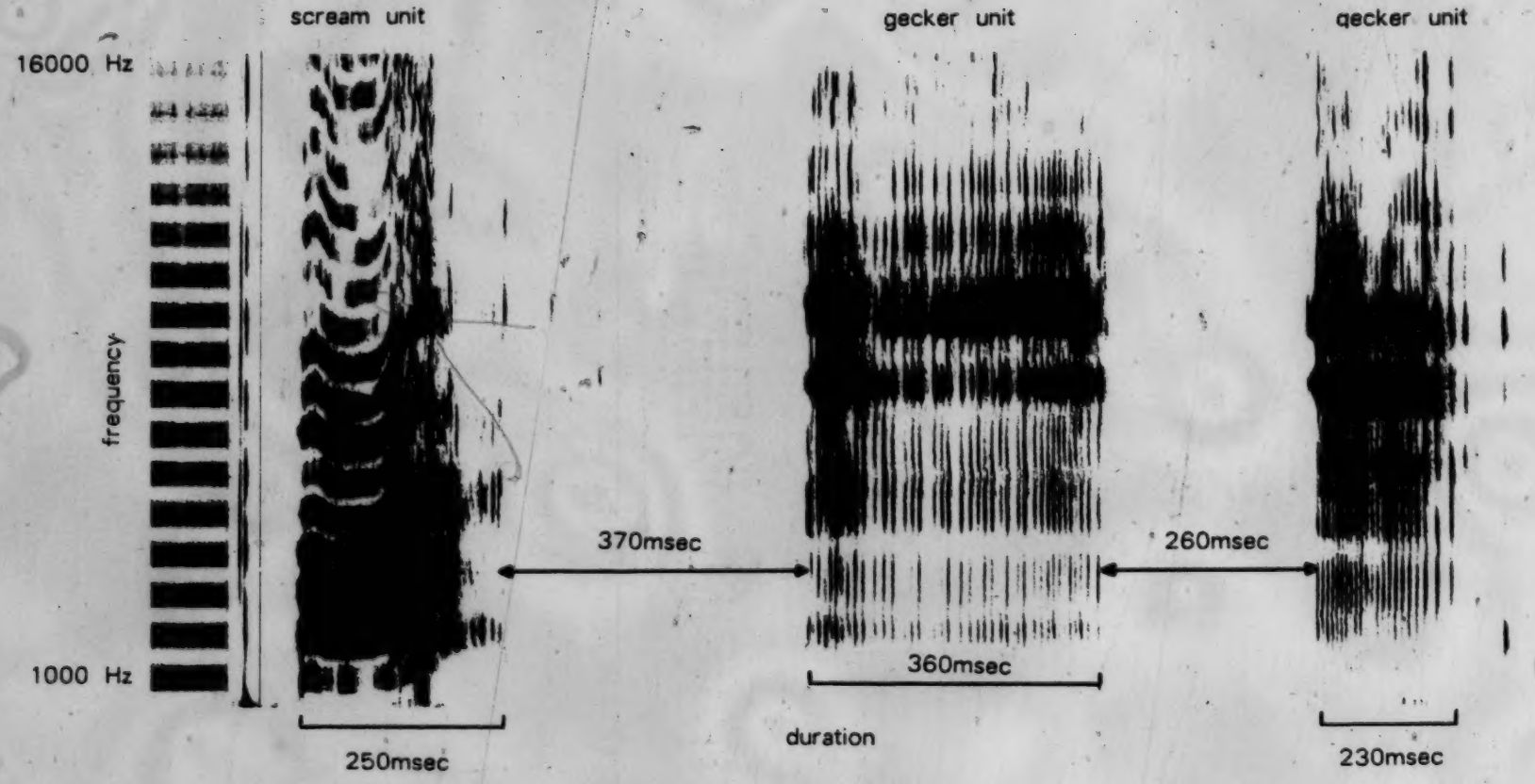


Fig 10. Wideband Sonagram of Scream/Gecker Vocalization

Interestingly, the Scream unit of a Scream/Gecker vocalization does not typically show a downglide of frequencies at offset, rather, the harmonics remain stable and, like Defensive Screams, the harmonic structure is somewhat smeared by accompanying wide band noise at the end of the unit. The "voice breaks" characteristic of Simple Screams do occur in Scream units of Scream/Geckers but are much less pronounced.

The Gecker components of a Scream/Gecker vocalization are morphologically similar to Gecker units in a Gecker vocalization, the major difference being that the Gecker component in a Scream/Gecker is much longer in duration (a mean of 400 msec, range 230 - 800 msec, N=4). The harmonic structure of the Gecker-unit in a Scream/Gecker is more pronounced due to the fact that vertical noise striations are less compact. As well, the most prominent bands of energy occur much higher up in the spectrum (8,000 - 10,000 Hz). (The concentration of energy at high frequencies necessitated the use of wide-band sonagrams from 80 - 16,000 Hz). As with simple Geckers, there is no noticeable frequency change throughout the Gecker-unit of a Scream/Gecker, even for units of very long duration.

b) Prolonged Geckers

This vocalization was initially identified as a compounded Gecker/Scream vocalization on the basis of gross perceptual characteristics. Analysis of the sonagrams of this vocalization suggests, however, that it is not a composite of two calls but rather a new call type. Prolonged Geckers (Figure 11) typically consist of an extremely protracted Gecker-unit described for Scream/Geckers above. The "protracted unit" consists of one unit of very long duration (mean duration is approximately 980 msec, range 800 - 1,200 msec, N=3).

With respect to distance propagation, Scream/Geckers and Prolonged Geckers must be considered intermediary between Hacks and Geckers which appear adapted for short range communication and Simple Screams which are better adapted for long range. The Scream-unit of a Scream/Gecker does show frequency change (typical of long-distance propagation) yet also shows abrupt onset/offset (more characteristic of short-range vocalizations). The protracted gecker-units would undoubtedly carry further than Hacks and Geckers, yet they do not show the specific acoustical adaptations for long-distance propagation evident in Screams and Scream/Geckers.

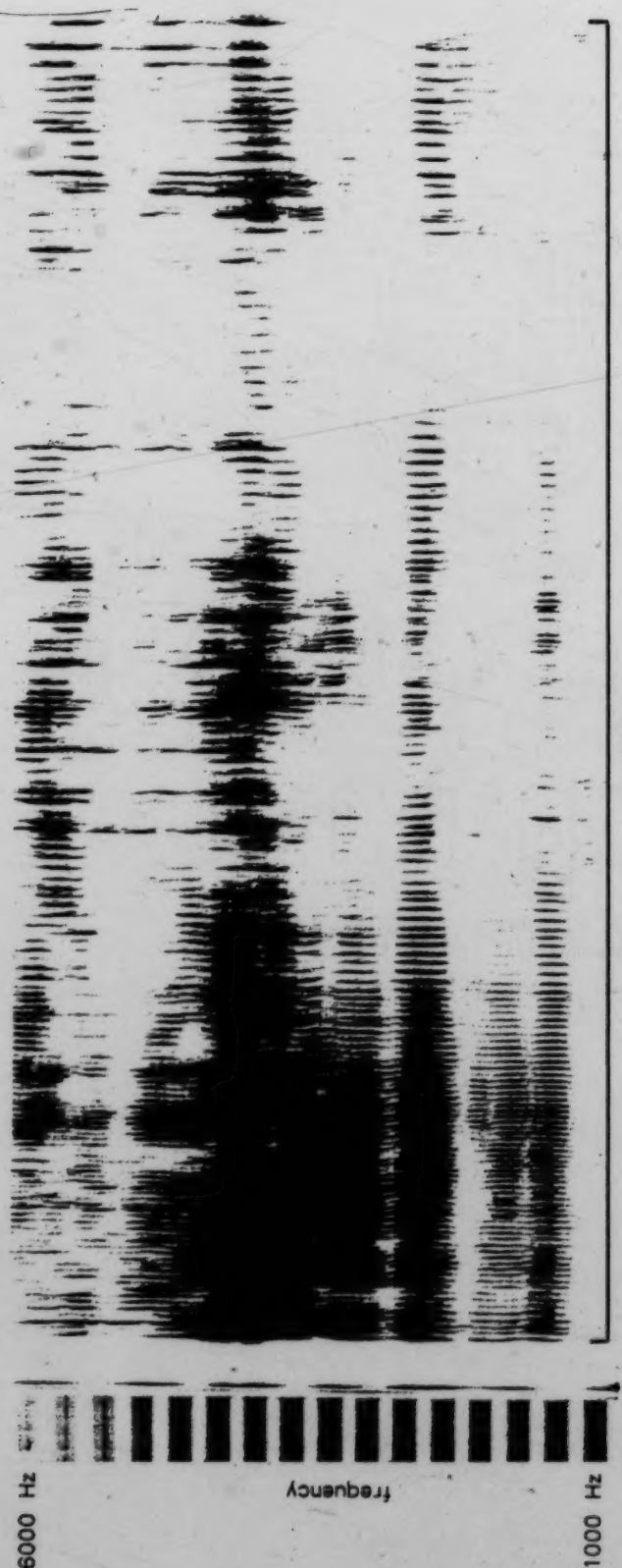


Fig 11. Wideband Sonagram of Prolonged Gecker Vocalization

The gradation represented from Hack to Gecker to the Prolonged Gecker may reflect increasing intensity along an emotional gradient (see Green 1975). The morphological changes that accompany a change in intensity along an emotional or motivational gradient warrant further investigation.

Other Calls

Female macaques utter a variety of other vocalizations in intervals between mounts, although the frequency with which they are employed is much lower than the calls described above. Very often, these vocalizations have specific contextual motivations.

1. Social Approach.

This vocalization is commonly given when a subordinate animal approaches a more dominant animal. In the case of a mating-bout, Social Approach vocalizations are usually emitted by a female who is approaching her partner after he has moved away.

The Social Approach vocalization is of very low intensity. (Recording of these vocalizations is difficult, given their low intensity and the fact that close proximity of the observer can inhibit the subordinate animal from vocalizing or even approaching a dominant animal). The Fo (approximately 300 Hz) is very prominent and does show modulation. Although there is evidence of harmonic energy at higher frequencies, it is very faint. (In some cases harmonic energy is barely visible, due mostly to low intensity of the call). Social approach vocalizations can be a single utterance of approximately 100 msec or a series of shorter utterances (a mean of 65 msec).

2. Contact Call.

The contact call is another very low intensity vocalization, uttered by the female when her partner leaves the vicinity during a between mount interval. The contact call is typically a single utterance of short duration (approximately 60 msec). As with Social Approach vocalizations, the Fo of the contact call (approximately 300 Hz) is often the only visible band of energy in the spectrum. In the case of Contact Call there is no frequency change.

Contact Calls can sometimes occur in conjunction with other vocalizations, most notably Geckers and Screams. Unlike the compound screams described above, however, the integrity of each call type is preserved (ie. contact and gecker-units are easily

destinguished and do not differ from independent utterences of each call type). The combining of different call types in a series may reflect ambivalent motivations on the part of the vocalizer. As described previously, non-consorting estrous females may often sit alone and emit a long series of vocalizations of different categories. It may be that Contact/Gecker and Contact/Scream combinations reflect an increase in motivation (frustration) when a female is attempting to reinitiate a sequence with a male who has deserted her.

3. Coo Call.

The Coo Calls recorded during intervals in mating bouts are those described by Green (1975) as "smooth late high" calls. Green states that this class of Coo call is used by estrous females during the later stages of courtship "in which the female decreases distance and follows closely, actively maintaining proximity" (Green: 1975:31). The Coo Calls emitted by females during intervals between mounts are often given by a female as she pursues a partner who has left her or after a partner has remained away for an extended period of time. The Coo Call is approximately 200 msec in duration. The Fo is between 300 - 500 Hz rising gradually to about 750 Hz by the end of the call. There is often an abrupt but slight jump in the Fundamental frequency reminiscent of the voice break described for Screams above. Bands of harmonic energy are clearly visible throughout the spectrum.

4. Threat.

The Threat vocalization is often given by a female following a chase sequence resulting in a disruption of the mating bout. The threat may be directed at the attacking male or non-directed as the female sits, recovering from the attack. (It may be the case that a female will give a Defensive Scream vocalization or a Threat vocalization depending on her dominance relationship to the attacking male: Defensive Screams with a dominant and Threats with a subordinate male). Threat vocalizations are also directed at "bystanders", i.e. juveniles or other, sometimes competing, females in close proximity to the consorting couple.

Threat vocalizations are uttered in a series. The unit durations are highly variable within a series (range 20 msec - 130 msec) as are the intervals between units (range 60 msec - 320 msec). The Fundamental frequency is very low (approximately 100 - 200 Hz)

and harmonic structures are obscured by intense wide band noise throughout the spectrum. Threat vocalizations are structurally similar to Geckers, the important difference being the irregularity of unit and interval durations during a Threat Vocalization.

5. Alarm Calls.

As described previously, females (especially in homosexual consorts) will sometimes approach an observer and threaten as a strategy for inciting a recalcitrant partner to mount. It is possible that the use of the Alarm call during a mating bout serves the same "incitory" function. The Alarm Call is of short duration (approximately 70 msec) which can be uttered singley or in succession. The Fo is very high, starting at about 1300 Hz, rising rapidly to a peak followed by a rapid down glide whith some wide band noise at offset. Energy is distributed at harmonics throughout the spectrum, even at frequencies above 8000 Hz. Alarm calls are well suited to distance propagation. They are, however, employed very infrequently by consorting females.

No comparison of Alarm Calls given by consorting females was made with Alarm Calls given by animals in non-mating contexts. However, Beer's (1965) work on the use of alarm calls by gulls in the mating context demonstrated that mating-related Alarm Calls were acoustically modified versions of the regular Alarm Call and these modified calls did not elicit the same response as regular Alarm Calls when played to animals outside the mating context. The work by Beer (1965) suggests a possible avenue for future research on mating-related and non-mating related Alarm Calls of Japanese macaques.

Discussion

Analysis of the acoustical properties of the kinds of vocalizations given by estrous females during intervals between bouts in a mating series suggests a differentiation of call types on the basis of distance propagation of sound. The distinction of "harsh" versus "clear" calls first suggested by Rowell and Hinde (1968) and later espoused by Brown (1982) seems to hold for the most frequently employed vocalizations: Hacks, Geckers, and Sceams.

Hacks and Geckers show the characteristics of "harsh" calls as described by Brown (1982): an overlay of wide-band noise which tends to obscure the harmonic structure of the call. As well, these calls characteristically show no change in frequency. The

importance of frequency modulation or change over the course of a call with respect to long distance propagation of sound has been demonstrated for both non-human primates (Brown 1982, Snowdon 1982) and for birds as well (Wiley and Richards 1980). Given the acoustical properties of Hacks and Geckers, it can be argued that these calls are designed for close range communication. Geckers can be seen as more intense than Hacks given that they are uttered in a series.

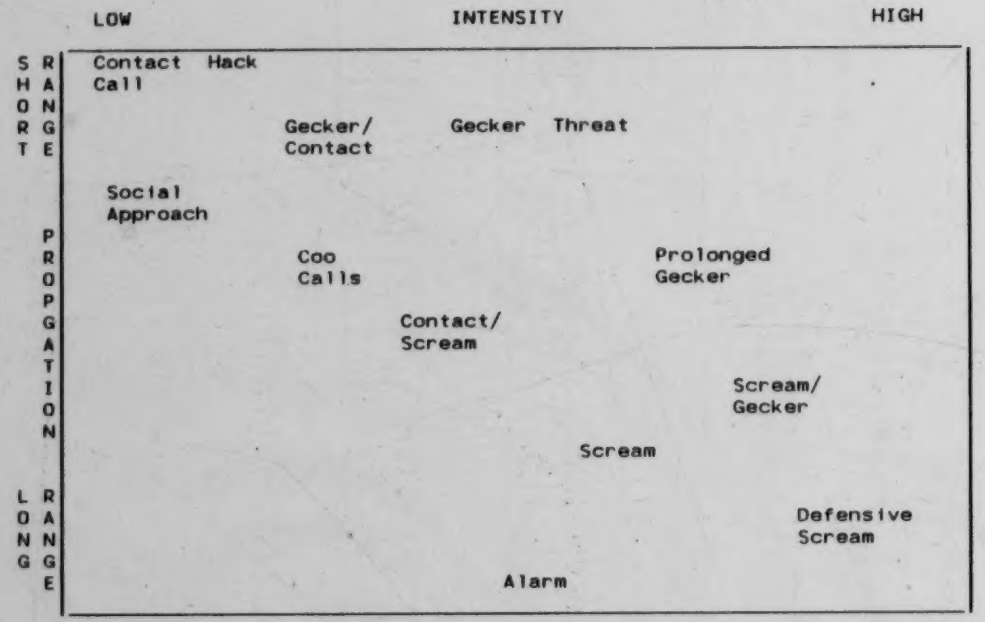
Simple Screams (and Defensive Screams), on the other hand, show the acoustical properties associated with distance propagation. They are akin to "clear" calls in that the harmonic structure is well defined, even though there is some wide band noise present. These calls have characteristically higher fundamental frequencies with considerable frequency modulation, which suggests that these calls will carry over a long distance than either Hacks or Geckers. The evidence of well defined energy peaks at high frequencies and evidence of abrupt jumps in the fundamental due to the glottis "breaking" suggests that Screams and Defensive Screams are very intense vocalizations (indicative of enhanced stress or motivation on the part of the vocalizer).

Prolonged Geckers and Scream/Geckers, appear to be intermediary forms between a) Hacks and Geckers and b) Simple Screams and Defensive Screams. Prolonged Geckers and Scream/Geckers are of greater intensity than Hacks and Geckers, as evidenced by longer call duration and generally higher Fundamentals. Despite the well defined harmonic structure of these calls, however, they do not show the the frequency modulation characteristics of Screams; so important in long distance propagation. Given that Scream/Geckers do contain a scream-unit reflecting the properties of Screams, they would have greater distance propagation than Prolonged Geckers.

Table 5 shows the location of all vocalizations given by estrous females in the mating context along two continuums: distance propagation (top to bottom) and motivational intensity (left to right).

A possible consequence of using long-range vocalizations as prompts during a mating bout is the increased potential for detection by other adult males. Long-range vocalizations have a potentially larger "audience" than calls designed for short-range communication. Detection of a consorting-couple by an adult male often results in disruption of the mating bout. Wiley and Richards (1982) indicate that unlike monogamous

Table 5 Vocalizations Along Intensity and Propogation Gradients



and polygynous species, colony-dwelling birds tend not to use long-distance vocalizations in the mating context. They suggest that the avoidance of long-range calls is a strategy designed to diminish the detection by competing males.

By analogy, it might be expected that female Japanese macaques will tend to employ short-range vocalizations with greater frequency than long-range vocalizations as prompts during a mating bout. It is possible, however, that the use of short-range vocalizations may be a learned behavior on the part of more experienced females, in which case an age difference in the use of short range vocalizations would be expected. Behaviorial analysis of the frequencies of different prompting behaviors supports this interpretation (see below). Finally, the influence of increased motivation on the part of a female (eg. increased frustration with a recalcitrant male) may override a tendancy to use short-range vocalizations. This is possible given that vocalizations indicating marked intensity seem to show a general increase in distance propagation.

B. Behavioral Analysis

Sociological Variables

1. Kinship:

The effect of kinship was measured using the non-parametric statistic Kruskall-Wallis One-Way Analysis of Variance (K-W). Results are summarized in Tables 6 and 7. There were no significant differences in the mean number of between-mount intervals for females of different kin-groups, nor in the mean interval duration, indicating that females of different kin-groups did not differ with respect to mating activity. As well, tests for differences between kin-related females in overall rates of non-vocal (T-Non), vocal (T-Voc) and total prompting behaviors (T-Prompt) were not significant (Table 6). Some significant results were found, however, with respect to the kinds of behaviors employed by kin-related females (Table 7). Of the non-vocal behaviors, the rate of ATM/MOR tended to differ between kin-groups ($p=.10$), suggesting that all kin-groups do not mount their partners equally as often. Of the vocalization categories, Scream Gecker differed significantly between kin-groups ($p=.01$) and the Compound Contact vocalizations tended to be different ($p=.10$).

Table 6 Differences in Mating and Prompting Behaviors

	KIN K-W X^2	P	AGE Spearman r_s	P	Parity K-W X^2	P	MatStat T-test T	P	Duration Spearman r_s	P	Partner T-test T	P
Number of Intervals	2.4	.79	-.09	.33	3.2	.20	-1.34	.19	---		---	
Interval Duration	8.2	.15	.18	.19	1.4	.71	-0.16	.88	---		1.59	.11
Total Non-Vocal	5.9	.31	.22	.15	2.2	.52	1.39	.18	.20	.17	-0.02	.98
Total Vocal	5.4	.38	-.01	.50	3.2	.37	0.31	.77	.50	.01 *	-1.36	.16
Total Prompting	6.1	.29	.29	.08 (*)	3.6	.37	0.65	.53	.38	.03 *	-1.24	.21

* = <0.05 Probability
(*)= >0.05 -0.10 Probability

Table 7 Differences in Specific Prompting Behaviors

	Kin K-W 2		Age Spearman		Parity K-W 2		MatStat T-test		Duration Spearman		Partner-Class T-test	
	X	P	r s	P	X	P	T	P	r s	P	T	P
ATM/MOR	9.33	.10 (*)	.41	.02 *	4.91	.18	-0.14	.89	.55	.00 *	-2.43	.02 *
TUL	5.99	.31	.02	.46	0.99	.80	0.65	.53	.06	.39	1.01	.31
OTHER (Non)	3.20	.67	.40	.03 *	8.26	.04 *	1.01	.34	.23	.14	1.12	.26
HACK	7.72	.17	.31	.06 (*)	1.55	.67	0.36	.72	.22	.15	0.50	.62
GECKER	3.15	.68	.07	.38	2.86	.41	-0.44	.67	.41	.02 *	-1.72	.09 (*)
PROLONGED GECKER	5.24	.39	.30	.08 (*)	0.75	.86	-0.79	.43	.61	.00 *	0.18	.85
SCREAM/ GECKER	14.61	.01 *	-.16	.23	0.38	.94	-0.89	.39	.45	.01 *	-1.05	.29
SCREAM	2.95	.71	.01	.49	0.59	.90	0.83	.43	.26	.10 (*)	-2.27	.02 *
COMPOUND CONTACT	9.13	.10 (*)	.41	.02 *	4.91	.18	0.68	.52	.47	.01 *	-1.52	.13
DEFENSIVE SCREAM	5.33	.38	-.17	.21	3.76	.29	-1.70	.10 (*)	.22	.15	-1.40	.16
CONTACT	7.67	.17	-.14	.26	0.69	.88	0.37	.75	.27	.10 (*)	0.84	.40
OTHER (Voc)	6.01	.31	.05	.40	0.89	.83	-1.69	.10 (*)	.55	.001 **	0.01	.99

(*) = >0.05-0.10
* = <0.05

From these results it might be argued that kin-related females have different propensities for specific kinds of behaviors. However, a cautionary note is in order. In all of the above cases, values were only obtained after a correction for ties in the mean ranks assigned to each group. Ties were the result of zero occurrence of behaviors for several groups. Given the complete absence of these somewhat infrequent behaviors (see Table 6, Chapter 3) for several of the kin-groups, the results from this study with respect to differences in frequency of behaviors between kin-groups may be due to a restricted sample. Thus, there is at best weak or inconclusive support for the hypothesis that kin-related females employ certain kinds of prompting behaviors more often than other groups.

2. Age:

The effect of age was tested using the non-parametric statistic Spearman's Correlation. The results are summarized in Tables 6 and 7. As with kinship above, there was no correlation with the mean number of between-mount intervals, nor the mean interval duration, again suggesting that females of different ages did not differ significantly with respect to mating activity.

The hypotheses that younger females vocalize more and older females employ more non-vocal behaviors were not supported as age did not correlate significantly with either T-Non or T-Voc. Interestingly, however, age did correlate with T-Prompt ($p=.08$) indicating that older females tend to prompt their partners more.

The failure of T-Non to correlate significantly with age is somewhat problematic in light of the fact that two of the three categories of non-vocal behaviors (Table 7) do correlate significantly with age: ATM/MOR ($p=.02$) and Other (non-vocal) ($p=.03$). The third category, TUL, did not even approach significance ($p=.46$). Removing TUL from the T-non calculation, i.e. lumping ATM/MOR and Other (non-vocal) behavior did yield a significant correlation with age; $p=.003$, $r=.5368$. This result would support the original hypothesis that older females employ more non-vocal behaviors than younger females.

While T-voc did not correlate significantly with age, a breakdown of the kinds of vocalizations given did yield some significant results (Table 7). The categories Hack ($p=.06$), Prolonged Gecker ($p=.08$), and Compound Contact ($p=.02$) correlated significantly

with age. These results suggest that there are age graded differences in the prompting behaviors used by females.

3. Parity:

Parity was tested using the K-W statistic. Parity did not yield any significant results with respect to mean number of intervals, interval duration, T-non, T-voc, or T-prompt (Table 6). The implications of these findings are that parity is not a strong predictor of variation in the behavior of females in the context under examination. Even a breakdown of the kinds of vocalizations yielded no significant results (Table 7). In the case of non-vocal behaviors, only the category Other (non-vocal) ($p=.04$) differed significantly between parity groups. However, a Spearman correlation between age and parity was highly significant ($r=.86$, $p=.001$), suggesting that the significant result achieved for parity is most likely a reflection of the influence of age.

4. Maternal Status:

The variable maternal status was tested using the Student's T statistic. Groups were comprised of those females with an infant from the 1981 birth season versus all other females. This variable was the least successful for predicting differences in the behavior of females. Maternal status showed no significant differences, at the level of total behaviors (Table 6), and only trends in differences at the level of specific vocalizations (Table 7). Females with infants showed a tendency to employ more Defensive Screams ($p=.10$) and Other (vocal) ($p=.10$), i.e. Social Approch, Threat, and Alarm Calls. These results are not altogether surprising, given that females are highly protective of their infants. However, females with infants did not differ from other females with respect to overall prompting activity. Maternal status can be seen as a poor predictor of the variation in prompting behavior exhibited by females.

Contextual Variables

1. Interval Duration:

The association of interval duration with rate of behavior was tested using the Spearman Correlation. Results are summarized in Tables 6 and 7. Duration proved to be the strongest predictor of variation in the behaviors of females. Both T-Voc ($p=.01$) and T-Prompt ($p=.03$) were significantly correlated with the duration of the between-mount interval. (Table 6)

Although duration did not reach significance for T-Non Voc, a break down of specific non-vocal behaviors showed that ATM/MOR was highly significantly correlated with interval duration ($p=.00$). In the case of specific vocalizations, every category except Hack ($p=.15$) and Defensive Scream ($p=.15$) was significantly correlated with interval duration (Table 7).

Intervals of long duration usually constitute irregularities in the mating sequence. Consequently it was hypothesized that females would prompt their partner's more during intervals of long duration. The strong correlation between interval duration and frequency of the behaviors lends support to the hypothesis that the behaviors employed by females in the intervals between-mounts function as prompts.

2. Partner Age-Class:

The effect of the male partner's age-class on the variation in the rate of behaviors employed by females was tested using the Student's T. The mean adjusted frequencies of behaviors directed at adult and sub-adult male partners were compared for all between-mount intervals. (Juvenile males were excluded from analysis due to low representation in the sample.) Results are summarized in Table 6 and 7.

A comparison of the means showed no significant differences between adult and sub-adult partners in the mean interval duration, although the difference did approach the .10 level of significance ($p=.11$), suggesting a possible trend for adult males to to have longer intervals. Adult and sub-adult partners did not differ with respect to the amount of prompting directed at them, as indicated by the non-significant results for T-Non, T-Voc, and T-Prompt (Table 6).

A breakdown of the specific behaviors did, however, produce differences in the behaviors directed by females at adult and sub-adult male partners. The category ATM/MOR was significantly different ($p=.02$) suggesting that females mount or attempt to

mount young males more frequently than adult males. With respect to vocalizations, sub-adult males tend to receive more Geckers ($p=.09$) and recieve significantly more Screams ($p=.02$). These results indicate that partners are treated differently by females on the basis of the male's age-class.

Discussion

Female Japanese macaques employ a variety of vocal and non-vocal behaviors in the intervals between mounts which communicate to the male the female's readiness to be mounted. As the interval between mounts increases, the rate at which certain of these behaviors are employed increases as well, suggesting that female's employ these behaviors to prompt the male. The fact that the rates of some behaviors do not increase with the duration of the interval suggests a possible gradation in intensity of the behaviors exhibited by females between mounts.

Some of the behaviors: TUL, Hack, and Other (non-voc), appear to be more generalized signals of female motivation. However, as the delays between mounts increase, females employ more "active" nonvocal behaviors such as mounting or attempting to mount their partner, and more acoustically intense vocalizations such as Prolonged Gecker.

Interestingly, the use of these more "volatile" (i.e. active or intense) signals are correlated with female age. Thus, it can be argued that older females exhibit stronger responses to delays in the mating sequence. Looking at those behaviors which do correlate with age further suggests that older females employ behaviors appropriate to the context: older females employ the low intensity Hack vocalization, and mild non-vocal signals as general indicators of receptivity, resorting to increased usage of more "volatile" signals as delays in the intervals between mounts increase in duration, which delays, if left unchecked, could result in a break-down of the mating bout. The acoustical nature of the vocalizations employed by young females, on the other hand, do not reflect differences in the intensity of the context, i.e. young females tend to employ the highly intense Scream vocalization even as a general indicator of receptivity in non-delayed intervals.

The use, by older females, of signals whose intensity are appropriate to the context, suggests that older females are more "sophisticated" or "adept" at exerting

influence over the situation. Older females exhibit a more elaborate strategy in order to influence male mating activity. Young females do not reflect this sophistication.

The results from the analysis of differences in the use of various behaviors employed by females to prompt their partners coincide with those of McDonald (1983), who found that older females were more "sophisticated" in their attempts to solicit a consort partner, than what Mcdonald characterizes as the "frantic" attempts of younger females. The tendency for older females to prompt thier partners more than do younger females,further supports the interpretation that older females are more active in attempting to influence the interactions in the mating context.

Finally, it is clear a female Japanese macaques does not behave equally towards each of her mating partners. It appears that females are more active and employ more intense signals in their attempts to influence the mating behaviors of younger males. This difference may reflect a difference in female "confidence"; females perhaps being less intimidated by younger males.

V. Conclusions

A. Discussion

The results from this study indicate that there are three major factors which influence variation in the frequency of vocal and non-vocal behaviors exhibited by female Japanese macaques during the intervals between mounts in a mating series. The first is the duration of the interval; the longer the interval, the greater the rate of the behaviors. The second most influential factor is the age of the female; younger and older females employ specific behaviors with different frequency. Finally, it was demonstrated that the frequency of different behaviors varied depending on the age-class of the female's partner. Other traditional variables such as kinship, maternal status and parity accounted for little of the observed differences between females. The results for duration, age and partner class describe the variation in behavior, however, the results in themselves are not self-explanatory. Without reference to the possible functioning of the behaviors with respect to series mounting and the mating system of Japanese macaques, the results remain at the level of description.

The model proposed for series mounting in rodents provides a useful framework in which to interpret the results of this study. As discussed earlier, studies of series mounting in rodents have demonstrated the importance of timing in the interactions between mating partners. It has been argued that regular stimulation of the females, through a series of repeated intromissions, induces widening of the cervix, which in turn facilitates the transport of sperm, thus increasing the likelihood of impregnation (Adler, 1969). The key issue is that the mounts in a series occur at regular intervals over time. Regular stimulation allows the slow build-up of hormones which, upon reaching a threshold, trigger the widening of the cervix.

Studies of rodent mating behavior further indicate that under normal or near-normal conditions, females exhibit behaviors which are said to regulate the timing of interactions, ensuring the optimal interval between mounts for the necessary build-up of hormones (McClintock, 1983). In the case of rodents, females retreat from males after a successful mount, employing avoidance strategies until sufficient time has elapsed, after which the female approaches a male (not always necessarily the same male), initiating a

subsequent mount.

In the case of Japanese macaques, partners remain in close proximity throughout the mating sequence. Females do not leave or attempt to avoid males between bouts, as in the case of female rodents. Rather, the results from this study indicate that female Japanese macaques regulate their mating interactions through a complex of vocal and non-vocal behaviors directed at the male. These behaviors communicate female motivation or readiness to be mounted. The fact that the frequencies of some of these behaviors increase with the duration of the interval suggests that the female employs certain behaviors to actively prompt or induce the male to mount.

The timing of mounts is a major factor in determining the behaviors of females. It is possible to hypothesize that there is an "optimal" or "preferred" interval between mounts; the female begins to indicate to the male her readiness to be mounted at or near the optimal interval, increasing her behavior as the duration of the interval exceeds the optimal time. In the sample for this study, the mean interval duration was 46.9 seconds and the modal interval was 27 seconds, (see Table 3, Chapter 2), suggesting an optimal interval somewhere between the two. However, the observed intervals between mounts are a result of an interaction between females and males. There is strong evidence from studies of series mounting in rodents that the optimal interval between mounts may be different for each sex (McClintock, 1982). Given two competing optimal intervals, resultant intervals in a mating sequence would essentially represent a compromise. From the fact that female Japanese macaques exhibit behaviors designed to prompt the male, rather than exhibiting behaviors designed to restrict male access at too early an interval following a mount, as has been reported for some rodent species, it is possible to hypothesize that the optimal between-mount interval for female Japanese macaques is shorter than that for her male counterpart. An obvious avenue for future research is determining the optimal intervals for female and male Japanese macaques. Is the optimal interval different? Is the optimal interval biologically fixed, i.e. the same for all females? What are the upper limits of the interval duration, after which females actively begin to intervene? These questions await further investigation.

The ability to answer the above, and other questions raised in this study are at present thwarted by ignorance of the physiological consequences of series mounting for

non-human primates. The failure of previous studies of macaque mating behavior to account for variation in female prompting behavior was due in large part to the fact that such research ignored the role of timing in the mating series, concentrating instead on the frequency of mounts (Michael and Zumpe, 1970). By analogy from the "rodent model", this study has shown that much about the behavior of female Japanese macaques during mating can be explained with reference to the duration of intervals between mounts. We can continue to look to studies of series mounting in rodents for further insights about macaque mating behavior.

For example, Edmonds et al. (1972) have demonstrated with rodents that, given a minimum number of mounts at regular intervals, the female is sufficiently stimulated to facilitate impregnation despite a considerable delay in the time at which she eventually receives an ejaculatory mount. Is this the case with Japanese macaques, as well? If so, could this fact help explain the the pattern of disruption of consorts by other males, i.e. the male attacks and chases the female, rather than her male partner. Are intruding males trying to gain access to already stimulated females? In general, what effect does disruption have on the female's physiology, i.e. does she lose the build up of stimulation she has been storing from previous mounts? Clearly, much more information about the physiological aspects of series mounting in non-human primates is required in order to analyze the impact of various forces on the mating activity of Japanese macaques.

The analogy between series mounting rodents and Japanese macaques breaks down, however, at the level of social structure and mating systems. Unlike macaques, which establish exclusive consort pairs, rodents alternate among a group of mating partners. The mounting strategies developed by female macaques and rodents would therefore be expected to differ, reflecting differences in the mating systems of the species.

While it is possible to predict the frequency of behaviors on the basis of interval duration, predicting the kinds of behaviors employed by females must take into account both the age of the female and the age-class of her partner. The results from this study show that females of different ages employ specific behaviors with different frequency. Females of different ages appear to employ different behaviors to indicate sexual motivation and/or elicit male mounting. Young females rely on a simple strategy,

employing the intensive scream vocalization, to indicate both motivation and to prompt a non-responsive male. Older females, on the other hand, employ low intensity vocal signals and subtle non-vocal behaviors to indicate sexual motivation, resorting to more intense vocalizations and more active non-vocal behaviors when males fail to respond.

Acoustical analysis of the vocalizations employed by females between mounts in a series shows a gradation along a continuum of increasing distance propagation and increasing intensity. The Scream vocalization is both intense and propagates over a long distance. The reliance of young females on the scream as the primary signal of sexual motivation may have serious repercussions for young females' mating success. The use of signals which propagate over a long distance, increases the chance of detection by other males, which in turn would increase the probability of disruption of the mating bout. Older females, employ more low intensity vocalizations, which do not propagate over a long distance, and would therefore not increase the risk of detection. Even in those delayed intervals in which older females employ more intense vocalizations, such as the prolonged gecker, the acoustical properties of these signals show them intermediary to the Scream on the distance propagation continuum (see Table 5, Chapter 4)

From the above results, an interesting question arises as to why younger females rely on intense vocal signals which by their very nature increase the the chances for detection and disruption by other males. A possible explanation is that younger females are actually trying to attract other males. Cox and LeBoeuf (1977) suggest that the copulatory vocalizations of females elephant seals (*Mirounga angustirostris*) function to attract other males, inciting male-male competition, thus constituting a mechanism of selection. The fact that female macaques return to their original partners following a disruption, would suggest that the vocal behavior of young females may not actually function to incite competition between males. However, there is good evidence from studies of macaque mating behavior that males who disrupt a consorting female are often eventually successful in establishing a consort with that female later in the season (Rostal and Eaton, 1982). Thus, it might be argued that young females, by employing long-range vocalizations during a consort with a male, may function to secure subsequent mating partners. The work by Baxter and Fedigan (1979) indicates that female Japanese macaques establish a number of consort partners with whom they mate from year to year.

Younger females are at a disadvantage in that they may not have established regualr mating partners. The vocalizations employed by young females during mating may therefore have long term benefits in securing mating partners, despite the short term costs of increased mating disruption.

One final aspect of the influence of age on the prompting behaviors of female macaques is the fact that older females tend to prompt their partners more than do younger females. Combined with the fact that older females are more likely to actually mount their partners, these findings suggest that older females are generally more active in their attempts to influence the timing of mounts in a series.

The results from this study have also shown that the behaviors exhibited by females vary depending on the age-class of the partner. Females treat sub-adult and adult males differently. It appears that females are likely to employ more intense or active signals with younger males: females are more likely to mount young males, and to use the intensive Scream and Gecker vocalizations as prompts.

A possible avenue for future research on Japanese macaque mating activity lies in the nature of male responses to female behaviors. During the course of my observations, I observed males attack or abandon female consort partners who had been persistent in their attempts to prompt the male. Negative responses to female prompting were not investigated in this study, however, where I observed these male "rebuffs" typically involved females who had been very vocal, characteristically employing screams or when attempting to mount an adult male. The hypothesis that males respond negatively to more intense prompting signals warrants further investigation in light of the results from this study that females use these behaviors less frequently with adult males.

The consequences of female prompting behavior on reproductive success warrants examination as well. If the goal of series mounting in Japanese macaques is not simply male ejaculation, but rather sufficient stimulation of the female prior to male ejaculation, then females have an interest in ensuring that they receive the requisite stimulation. In order to ensure this, females must play an active role in the timing of mounts in a sequence. However, if, in attempting to ensure the requisite stimulation, a female increases the risk of disruption of the series, either by antagonizing her partner or through interference from another male, the female could jeopardize her chance of

conceiving. Are their long term reproductive disadvantages which select against females who exhibit "volatile" patterns of prompting? Further investigations should consider the reproductive consequences of female prompting behaviors.

It is interesting to note that the variables kinship, parity, and maternal status, which have proven to be good predictors of variation in Japanse macaque behavior, are weak predictors of the variation in prompting behaviors exhibited by females, as indicated from the results of this study. McDonald (1983), too, found that these variables did not account for differences in females Japanese macaque courtship behavior. However, problems with the treatment of these variables in this study should caution against dismissing these variables altogether. The variables may may actually play a more important role in explaining differences in female prompting behavior than indicated from this study.

The analysis of the variable kinship in this study involved grouping females on the basis of major family lineages (extending from a core group of matriarchs over 20 years ago when the troop was first studied.) However, these major lineages have subsequently split into sub-lineages which can be recognized as distinct. For example, the Rheus lineage can be divided into at least three sub-groupings: Midori, Rotte, and Rheus. Given the limited sample of this study (N=25), numbers were insufficient to allow grouping of females on the basis of more closely related sub-lineages. Further investigations should be of sufficient sample size to permit analysis of kinship at different degrees of relatedness.

The variable maternal status was not found to be a powerful predictor of variation in this study, as well. It has been suggested that females having had an infant from the previous breeding season will have fewer and less intense estrous periods, exhibiting overall less-active sexual behavior; lactation being seen as a general hormonal supressant (Small, 1982). In this study, the frequecy of prompting behaviors employed by females who had had an infant in the previous (1981) birth season were compared against all other females. However, grouping all other females together ignores the fact that some females did not have an infant from the previous year due to their young age. Future research might better compare the behaviors of females with and without an infant within specific age or parity classes. The restricted sample of this study precluded analysis of

maternal status at this level. Another aspect of the variable maternal status not investigated in this study was the influence of the physical presence of an infant during a mating bout. Do females behave differently during mating when the infant is in close proximity or in physical contact with the female? Are the tendencies revealed in this study for females with infants to employ more defensive screams, social approach calls, etc., correlated with the actual physical presence of the infant? Future analysis should investigate these factors.

The final variable investigated, parity, again failed to account for variation between females. Given that parity was highly correlated with age, and age is a strong predictor of variation, the influence of age might tend to override any influence that parity might have on the behavior of females. A multivariate analysis might better determine the contribution of parity to variation in female prompting behavior. A further problem with parity exists with the category multiparous, which is the most heterogeneous both with respect to age and the total number of offspring a female has produced. A larger sample would facilitate finer differentiation of the multiparous category on the basis of the specific number of offspring .

One final variable, rank, warrants brief mention. The influence of differences in rank on the prompting behaviors of females was not investigated, owing to the lack of accurate data on rank for the females in this study. McDonald (1983) used a relative measure of rank: high, mid, low in her study, and found no correlation with differences in the courtship behaviors of females of different rank; suggesting, perhaps, that a finer descrimination in categories of rank is necessary. It is reasonable to hypothesize that the prompting behaviors of females will vary with respect to the rank of their partner relative to themselves. Do low ranking females behave differently with males of the same relative rank, as opposed to male partners of higher rank? However, determining rank in non-human primates is extremely problematic, and the influence of rank on other aspects of animal behavior is far from conclusive. (See for example Fedigan's (1983) review article on dominance and reproductive success.) The influence of rank on female prompting behavior must await further investigation.

B. Summary

Through analyzing variation in the frequency and use of behaviors exhibited by female Japanese macaques in the intervals between mounts in a mating sequence, it can be concluded that these behaviors serve to communicate to the male the female's readiness to be mounted. Furthermore, it can be concluded that there is modification in the prompting strategies of females over time. The observed ontogenetic differences between females may result from increased experience with the negative results of the use of volatile signals as prompts, both with respect to incidental detection and mating disruption by other males and the negative reactions of adult male partners to the use of these signals.

Investigating observed variation in the mating behaviors of female Japanese macaques not only identifies those sociological and contextual factors which influence their behavior, but the analysis of variation in behavior also reveals much about the nature of the Japanese macaque mating system.

Bibliography

Adler, N.T. 1969
Effects of the male's copulatory behaviour on successful pregnancy of the female rat. Journal of Comparative and Physiological Psychology, 69(4):613-622.

Adler, N.T., Resko, J.A., Goy, R.W. 1970
The effect of copulatory behaviour on hormonal change in the female rat prior to implantation. Physiology and Behaviour, 5,:1003-1007.

Altmann, J. 1974
Observational study of behavior: sampling methods. Behaviour,49:227-267.

Baxter, M.J. and Fedigan, L.M. 1979
Grooming and consort partner selection in a troop of Japanese monkeys (Macaca fuscata). Archives of Sexual Behavior,6(3):173-192.

Beer, C. 1976
Some complexities in the communication behavior of gulls. Annals of the New York Acadamy of Sciences, Vol. 280:413-432.

Bermant, G. 1964
Effects of single and multiple enforced intercopulatory intervals on the sexual behaviour of male rats. Journal of Comparative and Physiological Psychology,56:398-403.

Bramblett, C. 1976
Patterns of Primate Behavior. Mayfield Press, Palo Alto.

Brown, C.H. 1982
Auditory localization and primate vocal behavior.
In Primate Communication; Snowdon, C.T., Brown, C.H., and Petersen, M.R., (eds.). Cambridge University Press, London:144-164.

Carpenter, C.R. 1942
Sexual behaviour of free ranging rhesus monkeys (Macaca mulatta). Journal of Comparative Psychology, 33:113-142.

Cheney, D.L. and Seyfarth, R.M. 1980
Vocal recognition in free-ranging vervet monkeys. Animal Behaviour,28:362-367.

Cheney, D.L. and Seyfarth, R.M. 1982
How vervets perceive their grunts: field playback experiments. Animal Behaviour,30:739-751.

Chester, R.V. and Zucker, I. 1970
Influence of male copulatory behavior on sperm transport, pregnancy, and pseudopregnancy in female rats. Physiology and Behavior, 5:35-43.

Cochran, C.G. 1979

Proceptive patterns of behaviour throughout the menstrual cycle in female rhesus monkeys. Behavioral and Neural Biology, 27:342-353.

Cox, C., and LeBoeuf, B. 1977
Female incitation of male competition: a mechanism in sexual selection. The American Naturalist, 3: 317-335.

Deputte, B.L., and Goustard, M. 1980
Copulatory vocalizations of female macaques (Macaca fascicaloris): variability factor analysis. Primates, 21(1):83-99.

Doty, R. 1974
A cry for the liberation of the female rodent: courtship and copulation in rodentia. Psychological Bulletin, 81(3):159-172.

Drickamer, L.C. 1974
Social rank, observability, and sexual behavior of rhesus monkeys (Macaca mulatta). Journal of Reproductive Fertility, 37:117-120.

Dewsbury, D.A. 1981
Social dominance, copulatory behavior and differential reproduction in deer mice (Peromyscus maniculatus). Journal of Comparative and Physiological Psychology, 95(6):880-895.

Eaton, G.G. 1978
Longitudinal studies of sexual behavior in the Oregon troop of Japanese macaques. In Sex and Behavior, Status and Prospectus; T.E. McGill, D.A. Dewsbury, and B.D. Sachs, (eds.). Plenum Press, N.Y.:35-59.

Edmonds, S., Zoloth S.R. and Adler, N.T. 1972
Storage of copulatory stimulation in the female rat. Physiology and Behavior, 8: 161-164.

Fedigan, L.M. 1976
A study of the roles in the Arashiyama West troop of Japanese macaques (Macaca fuscata). Contributions to Primatology, Vol. 9, S. Konger, Basel.

Fedigan, L.M. 1982
Primate Paradigms. Eden Press, Montreal.

Fedigan, L.M. 1983
Dominance and reproductive success in primates. Yearbook of Physical Anthropology, 26: 85-123.

Fedigan, L.M., and Gouzoules, H. 1978
The consort relationship in a troop of Japanese monkeys. In Recent Advances in Primatology: Vol. 7, Behavior; D.J. Chivers and J. Herbert (eds.), Academic Press, Inc., London.

Goldfoot, D.A., Westerborg-van Loon, H., Groeneveld, W. and Koos Slob, A. 1980

Behavioral and physiological evidence of sexual climax in the female stump-tailed macaque (Maccaca arctoides). Science, 208:1477-1479.

Gouzoules, H. 1980
Biosocial determinants of behavioral variability in infant Japanese monkeys. University of Wisconsin, Ph.D. dissertation.

Gouzoules, H., Gouzoules, S., and Fedigan, L. 1983
Male Japanese monkey mating strategies: are female reproductive cues available? American Journal of Primatology, 4(4):344-345.

Gouzoules, H. and Goy, R. 1983
Physiological and social influences on mounting behavior of troop-living female monkeys (Macaca fuscata). American Journal of Primatology, 5: 39-49.

Gouzoules, S. and Gouzoules, H. (in press)
Mother's and other's responses to immature rhesus monkey screams. Animal Behavior.

Gouzoules, S., Gouzoules H. and Marler, P. (n.d.)
Rhesus monkey (Macaca mulatta) screams: representational signalling in the recruitment of agonistic aid.

Green, S.M. 1975
Variation in vocal pattern with social situation in the Japanese monkey (Mucaca fuscata): a field study. Primate Behavior, Vol 4 Developments in Field and Lab Research. Academic Press Inc., N.Y.

Green, S.M. 1981
Sex differences and age gradation in vocalizations of Japanese and Lion-tailed monkeys (Macaca fuscata and Macaca silenus). American Zoologist, 21:165-183.

Hamilton, W.J., and Arrowood, P.C. 1978
Copulatory voclaizations of chacma baboons (Papio ursinus), gibbons (Hylobates hoolock), and humans. Science, 200:1405-1409.

Hanby, J.P. 1972
The sociosexual nature of mounting and related behaviors in a confined troop of Japanese macaques (Macaca fuscata). University of Oregon, Ph.D. dissertation.

Hanby, J.P., Robertson, L.R., and Phoenix, C.H. 1971
The sexual behavior of a confined troop of Japanese macaques. Folia Primatologica, 16:123-143.

Hanby, J.P. and Brown, C.E. 1974
The development of socio-sexual behaviors in Japanese monkeys (Mucaca fuscata). Animal Behavior, 22:836-849.

Hymes, D. 1974
Foundations in Sociolinguistics: An Ethnographic Approach. University of

Pennsylvania Press, Philadelphia.

Itani, J. 1963
Vocal communication of the wild Japanese Monkey. Primates, 4(2):11-66.

Jolly, A. 1972
The Evolution of Primate Behavior. MacMillan Publishing Co. Inc., N.Y.

Krieger, M.S., Orr, D., and Perper, T. 1976
Temporal patterning of sexual behavior in the female rat. Behavioral Biology, 18:379-386.

Labov, W. 1972
Sociolinguistic Patterns. University of Pennsylvania Press, Philadelphia.

Lehner, P.N. 1979
Handbook of Ethological Methods. Garland STPM Press, N.Y.

Lieberman, P. 1977
Speech Physiology and Acoustic Phonetics. MacMillan Publishing Co. Inc., N.Y.

McClintock, M.K. 1981
Simplicity from complexity: a naturalistic approach to behavior and neuroendocrine function. New Directions for Methodology of Social and Behavioral Science, 8:1-19.

McClintock, M.K., and Adler, N.T. 1978
The role of the female during copulation in wild and domestic Norway rats. (Rattus norvegicus). Behavior, 67:67-96.

McDonald, M. 1983
The courship behaviour of female Japanese monkeys. McMaster University, Master's Thesis.

Michael, R.P. and Zumpe, D. 1970
Sexual initiating behavior by female rhesus monkeys (Macaca mulatta) under laboratory conditions. Behavior, 36:168-186.

Michael, R.P., and Zumpe, D. 1971
Pattern of reproductive behavior. In Comparative Reproduction in Non-Human Primates; E.S.E. Hafez (ed.). C.C. Thomas, Springfield, pp. 205-242.

Modahl, K.B., and Eaton G.G. 1977
Display behavior in a confined troop of Japanese macaques (Macaca fuscata). Animal Behavior, 25:525-535.

Nie, N.H., Hull, C.H., Jenkins, J., Steinbrenner, K., and Bent, D.H. 1975
Statistical Package for the Social Sciences (Second Edition). McGraw Hill, Inc., N.Y.

Nigi, H. 1976
Some aspects related to conception of the Japanese monkey (Macaca fuscata). Primates; 17(1), 81-87.

Nigi, H., Tiba, T., Yamomato, S., Floescheim, Y., and Ohsawa, N. 1980.
Sexual maturation and seasonal changes in reproductive phenomena of male Japanese monkeys (Macaca fuscata) at Takasakiyama. Primates, 21(2):230-240.

Rostal, D.C., and Eaton, G.G. 1983
Puberty in male Japanese macaques (Macaca fuscata): social and sexual behavior in a confined troop. American Journal of Primatology, 4:135-141.

Rowell, T.E. 1962
Agonistic noises of the rhesus monkey (Macaca mulatta). Symposia of the Zoological Society of London, 8:91-96.

Rowell, T.E., and Hinde, R.H. 1962
Vocal communication by the rhesus monkey (Macaca mulatta). Proceedings of the Zoological Society of London, 138:279-294.

Saayman, G.S. 1970
The menstrual cycles and sexual behavior in a troop of free-ranging chacma baboons (Papio ursinus). Folia Primatologica; 12, 81-110.

Small, M.F. 1982
Reproductive failure in macaques. International Journal of Primatology, 2:137-147.

Snowdon, C.T. 1982
Linguistic and phycholinguistic approaches to primate communication. In Primate Communication. Snowdon, C.T., Brown, C.H., and Petersen M.R. (eds.), Cambridge University Press, London, pp. 211-238.

Snowdon, C.T., Brown, C.H., and Petersen, M.R. (eds.) 1982
Primate Communication. Cambridge University Press, London.

Stephenson, G.R. 1973
Testing for group specific communication patterns in Japanese macaques. Precultural Primate Behavior, Emil W. Menzel (ed.). Symposia of the Fourth International Congress of Primatology (Vol. 1), S. Karger, Basel.

Struhsaker, T.T. 1967
Auditory communication among vervet monkeys. In Social Communication Among Primates. Altman, S. (ed.). University of Chicago Press, pp. 281-324.

Takahata, Y. 1980
The reproductive biology of a free-ranging troop of Japanese monkeys. Primates, 21(3):303-329.

Thibault, P. (ed.) 1979
Le Francais Parle: Etudes Sociolinguistiques. Linguistic Research, Inc., Edmonton,

Alberta.

Tokuda, K. 1961
A study of the sexual behavior in the Japanese monkey troop. Primates, 3(2):1-40.

Waser, P. 1975
Experimental palybacks show vocal mediation of intergroup avoidance in a forest monkey. Nature,255:56-58.

Waser, P. and Waser, M. 1977
Experimental studies of primate vocalization: specializations for long-distance propagation. Zeitschrift fur Tierpsychologie,43:239-263.

Wiley, R.H., and Richards, D.C. 1982
Adaptatins for Acoustic communication in birds: sound transmission and signal detection. In Acoustic Communication in Birds; Kroodsma, D.E., Miller, E.H., and Ouellet, H. (eds.). Academic Press, N.Y., pp. 131-212.

Wolfe, L.D. 1976
Sexual behavior of the Arashiyama West Troop of Japanese macaques (Macaca fuscata). University of Oregon, Ph.D. dissertation.

Wolfe, L. 1979
Sexual maturation among members of a transported troop of Japanese monkeys (Macaca fuscata). Primates, 20(3):411-418.

Zumpe, D. and Michael, R.P. 1968
The clutching reaction and orgasm in the female rhesus monkey (Macaca mulatta). Journal of Endocrinology, 40:117-123.

Zumpe, D. and Michael, R.P. 1970
Ovarian hormones and female sexual invitations in captive rhesus monkeys (Macaca mulatta). Animal Behavior, 18:293-301.

Zumpe, D., and Michael, R.P. 1977
Effects of ejaculations by males on the sexual invitations of female rheus monkeys (Macaca mulatta). Behavior, 60(3-4):260-277.